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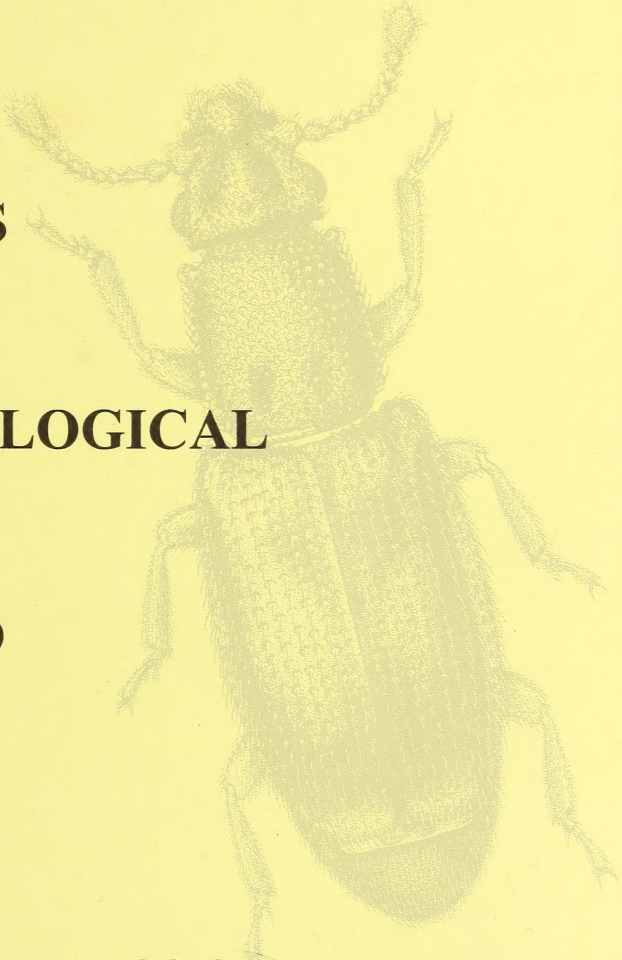

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Cover illustration: *Monotoma picipes* Herbst. Artist: Roelof Idema.

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ENTOMOLOGICAL SOCIETY OF ONTARIO

Volume 130 ***1999***

From the Editor,

Changes in publication technology, distribution methods, and costs are still exerting stress on the way in which we scientists communicate. The Proceedings are no exception in being affected by such changes. The ESO is concerned about a number of problems we are experiencing in this respect. The production cost of the Proceedings is going up, the number of subscribers is going down, and a gamut of new publication options to deal with these problems is being spawned by the digital information age. Ignoring such problems and opportunities could lead to the inevitable demise of our journal. However, there is no great urgency, since the current method of production of the Proceedings is still within the means of the Society. Furthermore, committing ourselves to some form of electronic publication is in my opinion still premature for three reasons. The first reason is that it is not as yet cheaper. The second reason is that the technology is evolving so rapidly, that a commitment now could be unnecessarily costly, and may have to be changed or even reversed in the near future. The final reason is that too few of our members have the up-to-date hardware to receive, display and print high quality figures as yet. Whereas the appropriate methods for full electronic publication are certainly available, the penetration of the necessary technology, and the willingness of the scientists to embrace it, is inevitably going to face some delays.

In the meantime, Kevin Barber, our current president, is conducting an intensive review of the entire publication procedure (and associated costs) of the Proceedings. I believe that with some minor increases in efficiency, and some cost cutting, we should be able to keep producing a high quality, printed journal for at least another three to five years. However, I am still keen to offer our members an opportunity to experiment with electronic publishing. I have decided to invite anyone who has recently published a taxonomic revision, annotated checklist, or survey in the Proceedings, to publish an update or revision at minimal cost. Such a revision will consist of a title, abstract and introduction (total 2-3 pages) in the Proceedings, as well as a full-length, refereed, detailed new version of the entire paper on the ESO web-site. This cannot include the description of new species, since electronic publishing is not as yet an acceptable medium for publishing new species. The ESO will guarantee to keep the paper on its web-site for at least five years.

This year's volume continues with a general trend towards a growing emphasis on bio-diversity. Two key papers dominate this volume; one by Yves Bousquet and Serge Laplante, on the beetle genus *Monotoma*; the other by John Huber and Lin Naiquan on the Hymenopteran *Camptoptera* group of genera in the Mymaridae. I am glad the Proceedings have the opportunity to publish this work, based on solid, traditional taxonomy. That way we confirm the importance of taxonomic

research in an age in which too many people talk about bio-diversity, without possessing the detailed knowledge of the relevant taxa to come to authoritative conclusions. Three shorter contributions show how a solid knowledge base in taxonomy can be used to further our understanding of the role of certain insects in natural and managed ecosystems. Bruce Broadbent and co-workers record three parasitoids of the tarnished plant bug, new for Canada. Terry Wheeler and co-workers describe the range expansion of holarctic Opomyzid flies into the nearctic region. Chris Darling describes the fascinating life history of a Parilampid parasitoid of a deathwatch beetle.

The breadth of research interests of our members is illustrated by the inclusion of a paper by Hasan Tunaz and David Stanley on the immune system of the American cockroach. Five reviews of recently published entomological texts round out this volume. I hope our readers will once again agree with me, that with our Proceedings the membership of the ESO is making a significant contribution to the science of entomology.

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LIFE HISTORY AND IMMATURE STAGES OF *STEFFANOLAMPUS SALICETUM* (HYMENOPTERA: CHALCIDOIDEA: PERILAMPIDAE)

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Abstract *Proc. ent. Soc. Ont.* 130: 3-14

The life history and immature stages of *Steffanolampus salicetum* (Hymenoptera: Chalcidoidea: Perilampidae) are described for the first time based on field studies in a mixed hardwood forest in southern Ontario. *Steffanolampus salicetum* females were collected on a windblown maple tree and subsequent examination of wood samples in the laboratory revealed that this wasp is a primary parasitoid of *Ptilinus ruficornis* (Coleoptera: Anobiidae). Both the oviposition behaviour and the morphology of the first-instar or planidial larva are unique in Perilampidae but the structure of the egg is virtually identical to *Perilampus*. The phylogenetic implications of these results are discussed. Rates of *Ptilinus* parasitism by *Steffanolampus* are low, which suggests that there is very little potential for the use of these parasitoids as agents of biological control.

Introduction

Steffanolampus is the only endemic genus of Perilampidae in the Nearctic region (Darling 1997). It did, however, take considerable time and effort to establish this most basic distributional fact. As documented in considerable detail by Peck (1974), the type and only included species (*Perilampus salicetum* Steffan) was originally described from material collected in Austria before 1877. This species has not been collected in Europe in the intervening 120 years and although the circumstances surrounding the introduction remain unclear, it is almost certain that the type specimens were the result of an infestation of wood imported from North America. Peck (1974) also provides a detailed treatment of the distribution and host associations of *Steffanolampus* and notes its association with maple trees (*Acer* spp.) infested with anobiid beetles. However, the exact nature of this host association, that is, whether the wasps are primary parasitoids of xylophagous beetles or hyperparasitoids associated with these beetles, has remained elusive. This is surprising because these chalcidoid wasps are rather large (females are up to 5 mm in body length) and have a distinctive appearance. The females have upturned ovipositors and raised processes on the pronotum, both of which facilitate easy identification (Darling 1997, p. 540, fig. 6).

In recent years considerable progress has been made in elucidating the phylogenetic affinities of the chalcidoid wasps with planidial first-instar larvae, Perilampidae (*sensu* Darling 1997) and Eucharitidae (*sensu* Heraty 1997). Much of this progress is a result of the discovery of the life history and immature stages. The egg and first-instar larva of both of these families are unique in Chalcidoidea. The eggs are laid in or on plant material some distance from the host (cf. in, on, or in very close proximity to the host), and the first-instar larvae are heavily sclerotized, active planidia, "minute wanderers" (*sensu* Smith 1912) that either find and attack the host directly or attach to an intermediate host (cf. relatively inactive hymenopteriform larvae that begin feeding on the host

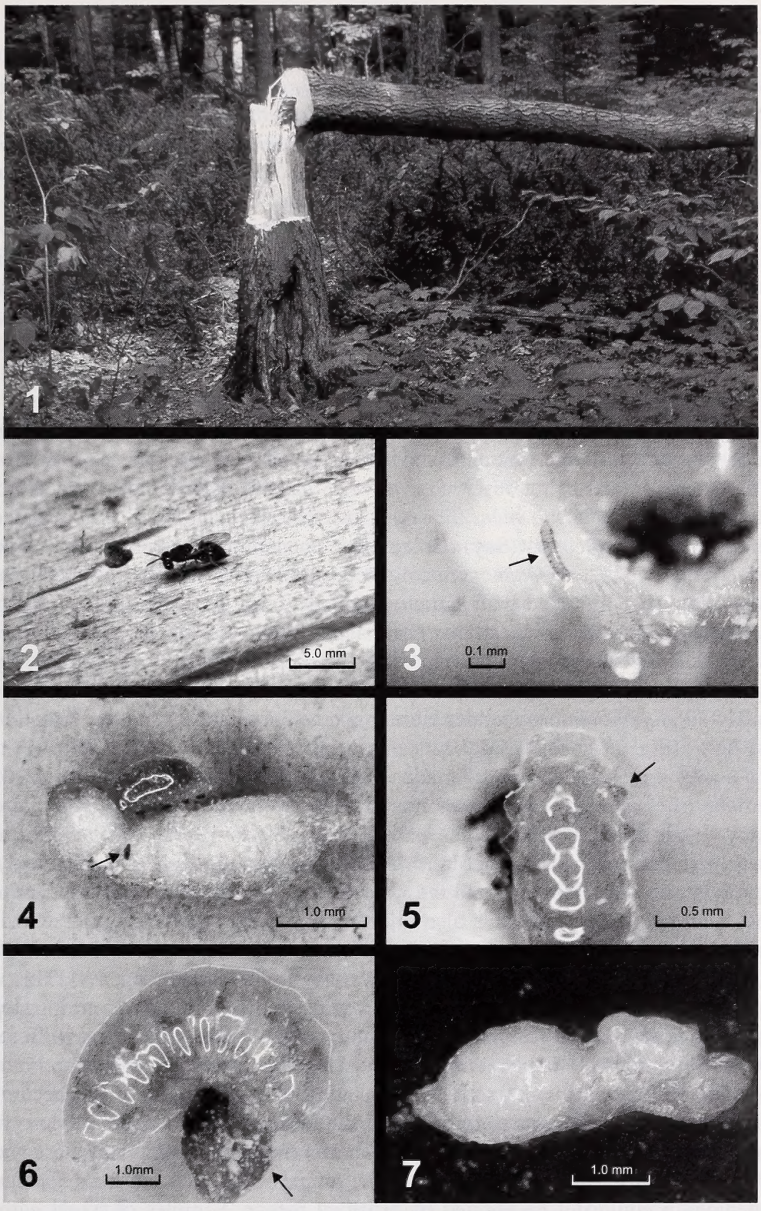
shortly after eclosion from the egg). There is good published information on the life history and immature stages for three of the five subfamilies of Eucharitidae (Darling 1992; Heraty 1994) and for the perilampid subfamily Chrysolampinae (Darling and Miller 1991). The greatest gaps in our knowledge concern the Perilampinae. Of the six described genera, published information is available for only *Perilampus* Latreille (Bergold and Ripper 1937; Clancy 1946; Principi 1947; Tripp 1962; Tanton and Epiala 1984; Heraty and Darling 1984) and for *Krombeinius* Bouček (Darling 1995). Three of the four genera for which there is no published information on life history and immature stages are associated with woodboring beetles (*Steffanolampus, Monacon* Waterston, and *Burksilampus* Bouček, cf. *Euperilampus* Walker which are generally considered to be hyperparasitoids of Lepidoptera through Ichneumonidae; see Darling 1997). Xylophagous beetles are particularly interesting hosts for parasitoid Hymenoptera because wood-boring beetles are the likely hosts in which parasitoidism originated (Quicke 1997). In addition, xylophagous beetles are the ancestral hosts of many clades of parasitoid wasps and of many enigmatic and relictual families of parasitoids (e.g., Orussidae, Vanhorniidae, Stephanidae, Megalyridae; Goulet and Huber 1993). Both the host association and morphological features of *Steffanolampus* suggest that information on the life history and immature stages of *Steffanolampus salicetum* could provide valuable information on the phylogeny of the Perilampinae and hence Perilampidae.

Methods

Field studies and collections were conducted at the Joker's Hill property of the University of Toronto (Canada, ON: York Region, NW of Newmarket and S of Hwy 9, 44° 03' N, 79° 29' W, 300m). This property is an ecologically significant area in the Oak Ridges Moraine and contains a mixture of habitat types including quality old growth forest (see http://www.erin.utoronto.ca/~w3pkota/jh.html for more detailed information and a map of the study area). The specific study site was located on the eastern half of the property (E of Dufferin Street), in an area of mixed hardwood forest (sugar maple, *Acer saccharum* Marsh; red maple, *Acer rubrum* L.; American beech, *Fagus grandifolia* Ehrh.; and yellow birch, *Betula allegheniensis* Britton). The field collections and observations were made in 1997 and 1998 and centered on a windblown maple tree (*Acer saccharum* Marsh). The tree fell in a windstorm in the spring of 1997 (Bill Fox, pers. comm.) and shattered in a way which exposed a considerable area of heartwood (Fig. 1). Weekly observations were also made at woodpiles of beech and maple at the study site from 25 June to 23 August 1997, both before and after *Steffanolampus* was first encountered, allowing for rather precise data on the flight time of the adults of both host and parasitoid. A detailed photographic record of the observations was made by the author and form the basis for drawings provided herein. The identifications of the parasitoid as *Steffanolampus salicetum* and the host as *Ptilinus ruficornis* Say were made by the author, and the latter was confirmed by Dr. Donald Bright, Research Branch, Agriculture and Agri-Food Canada, Ottawa.

Specimens and samples of the wood were brought back to the Royal Ontario Museum (ROM) for *ex situ* behavioural studies, rearing and dissection. Wood samples either were kept continuously at room temperature or overwintered outdoors and brought indoors in April 1998 and reared at room temperature. Wood samples from the field with beetle entrance tunnels were examined with a stereomicroscope for eggs and planidia, and the wood was subsequently split open along the length of the tunnel and monitored for activity. Immature stages were preserved in 80% ethanol or slide-mounted.

Beetle larvae were maintained in petri dishes of various sizes for observation. The observation dishes contained blocks of wood of varying sizes with either naturally occurring galleries or holes drilled to accommodate grubs. Observation dishes were maintained at room temperature although photoperiod and humidity were not controlled.



FIGURES 1–7. 1. Windblown sugar maple tree, showing exposed heartwood, the site of attack by *Ptilinus ruficornis*. 2. *Steffanolampus salicetum* female examining entrance holes of *P. ruficornis*; note: female beetle is partially emerged from the hole, and exhibiting guarding behaviour. 3–7. Immature stages of *S. salicetum*. 3. First-instar or planidium (arrow) attached to frons of late instar larva of *P. ruficornis*. 4. Second-instar feeding on host prepupa; note: exuvium of planidium (arrow). 5. Early third-instar; note: fleshy protuberances (arrow). 6. Late third-instar; note: shriveled remains of host (arrow). 7. Female pupa.

Eggs and first-instar larvae of *S. salicetum* were examined with a combination of compound microscopy (phase and interference contrast) and scanning electron microscopy (SEM). Slides were prepared using Hoyer's medium both with and without clearing of the immature stages for 4 hours in Nesbitt's solution (eggs, DCD Slide Nos. 1981, 1982, 2047, 2049; planidia, DCD Slide Nos. 1983–1996, 1998–2000). Planidia were critical point dried before examination by SEM (DCD SEM Nos. 474–478, 483–490). Descriptions of the egg and planidium are a composite of multiple specimens examined with both SEM and light microscopy. A photographic archive of the behaviours and the dissections is maintained at the ROM.

Terms for morphological structures of the first-instar larva follow Heraty and Darling (1984). Voucher specimens of adult *S. salicetum* and *P. ruficornis*, and slide-mounted and SEM-prepared eggs and first-instar larva of *S. salicetum* are deposited in the ROM entomology collection.

Results

Natural History Observations of *Steffanolampus salicetum* and *Ptilinus ruficornis*

1997: *Steffanolampus* were first observed and collected on a mixed beech/maple woodpile on 17 July. This woodpile was being observed every 3–5 days in order to collect specimens and life history information on *Vanhornia eucnemidarum* Crawford (Hymenoptera: Vanhorniidae) and their recorded host *Isorhipis ruficornis* (Say) (Coleoptera: Eucnemidae), which were first collected on 25 June. Five females of *S. salicetum* were collected (no males were observed) and returned to the ROM, where they were provided with samples of wood from the woodpile and dampened filter paper in an attempt to induce oviposition. These females and substrates were observed daily for between seven and ten days; no eggs or oviposition behaviour was observed. On 20 July the wind-blown sugar maple was found. The exposed heartwood had many 2–3 mm entrance holes and approximately 20 *Steffanolampus* females were found walking on exposed heartwood in the vicinity of these holes (Fig. 2). A few adult beetles were present on the wood but most of the *Ptilinus ruficornis* females were in the wood. Females were usually visible 2–3 mm inside the entrance holes. No males of *P. ruficornis* were encountered on the wood. Females of *Steffanolampus* would approach and antennate the entrance holes leading to tunnels formed by *Ptilinus* females. If a live female beetle was present in the tunnel in a "head out" orientation, she would quickly thrust her head and pronotum out of the tunnel and the wasp would move off and investigate other entrance holes. This "guarding behaviour" was also elicited by putting small slivers of wood above the entrance hole. In the absence of a guarding response by the female beetle, the *Steffanolampus* female would turn around and slowly walk backwards into the tunnel (Fig. 4A). This was a slow, apparently deliberate behaviour and the female would stay in the hole at varying depths (up to about three-quarters of the body length), with its body slowly rocking back and forth for up to one minute. On 25 July, *Steffanolampus* females were still present on the maple wood but in smaller numbers; no *Ptilinus* females were actively excavating tunnels (frass was not accumulating beneath the holes) but a few were guarding in response to inspection by *Steffanolampus* females. On 10 August, *Steffanolampus* females were not present on the maple stump and there was no beetle activity. Dead *Ptilinus* females were present in the tunnels; there was no frass accumulation and guarding behaviour could not be elicited by artificial means. Samples of wood with holes and entrance tunnels were collected on 25 July and 10 and 23 August and returned to the ROM for inspection and dissection. This wood was split parallel to tunnels (as in Fig. 4) and both the exposed surface of the wood and the inner surfaces of the tunnels were examined for immature stages of the host and parasitoid. None were found on the 25 July samples after an extensive search of 6 tunnels using a stereomicroscope. These wood samples were subsequently examined every 2–3 days for activity. On 5–7 August, planidia were found crawling on the walls of one

tunnel and some planidia had their heads burrowed into the walls of the gallery; many dead planidia were also found. This wood was then split radially around the hole and small eggs were found imbedded in the wood (Fig. 4C). These eggs were located 0.7 to 1 mm from the wall of the tunnel. Also, very elongate beetle larvae (length, 1.5 mm; width approximately 0.08 mm) were found in the heartwood, approximately 2.25 mm from the wall of the tunnel at a depth of approximately 3.25 mm and oriented parallel to the grain of the wood (Fig. 4E). These larvae (DCD Slide Nos. 1997, 2001) are virtually identical to the first-instar larva of the European species *Ptilinus pectinicornis* (L.) illustrated by Cymorek (1971) and are regarded as the first-instar larvae of *P. ruficornis*. On 23 August, a sample of the wood with beetle holes was collected from the stump and dissected at the ROM. Beetle larvae were found in the wood; they were small (approximately 0.4 mm), C-shaped scarabaeiform grubs virtually identical to the second-instar larvae illustrated by Cymorek (1971). One of these larvae had a planidium attached to the venter of the thoracic region (as in Fig. 4G).

1998: The maple tree was visited regularly during the summer. An emergence trap was erected over the stump on 11 June and monitored weekly until the end of July; no *Ptilinus* nor any *Steffanolampus* were collected. In addition, neither beetle nor wasp activity was noted on the log on any of the 7, 11, 15, or 23 July visits.

Wood samples were dissected in the spring of 1998. On 5 April, the wood kept at room temperature was cut into approximately 3 cm sections across the grain. Many of these sections were riddled with galleries and frass and many large (4–5 mm) C-shaped grubs were collected. A few adult beetles and pupae were also found in the wood. These beetle larvae were examined for planidia. Planidia were found on only two larvae of approximately 30 larvae. One beetle larva had a single planidium on the venter and the second had two planidia, one ventrad and one attached to the gena (Fig. 3). The beetle larvae were still actively feeding and tunneling in the wood and were maintained in observation dishes. These were observed every few days. One larva with planidium was preserved on 27 April and the second larva and its planidium were still alive on 8 September; however these were found dead in February 1999. Additional samples of wood were dissected in July and August 1998; large numbers of *Ptilinus* (P) were found (larvae, pupae and adults) but very few had *Steffanolampus* planidia (S): 18 July (32P, 1S), 5 August (42P, 4S), 18 August (34P, 1S), 19 August (27P, 0S), 20 August (23P, 0S; 11P, 0S). In addition, *Ptilinus* adults, but no adult *Steffanolampus*, emerged in the containers with the wood samples. These data indicate that the parasitism rate by *Steffanolampus* is less than 3.5%. In May 1999, *P. ruficornis* were still emerging from the wood samples collected in August 1997 and March 1998; 59 adult beetles of both sexes and five larvae emerged in the period between September 1998 and May 1999. No *Steffanolampus* were recovered which provides additional evidence of the low level of parasitism.

In June, 1999 a subsample of the lab-reared infested wood was again dissected. On 20 June, a prepupa of *P. ruficornis* was collected with an attached parasitoid larva (Fig. 4). The larva was about 1.2 mm in total length and the head was deeply imbedded into the body of the host. On the basis of size and the presence of the planidial exuvium, this is regarded as the second-instar larva of *S. salicetum*. On 22 June, the parasitoid was 3.25 mm in length and different in appearance, i.e., there were distinct lateral protuberances present on the thoracic segments (Fig. 5). Although no exuvium was recovered, this is regarded as the early third-instar. The larva was feeding completely externally and the host was still largely intact. By 27 June the parasitoid had increased to 5 mm in length and had almost completely consumed the host (Fig. 6); this is regarded as the late third-instar and the lateral protuberances are no longer visible. The mouthparts were disengaged from the host tissues and the nondescript hymenopteriform grub was quiescent on the host. On 28 June, the larva voided its meconium and shrunk in length to 4.5 mm. The prepupal stage lasted about 24 hours and on 29 June a white female pupa was present (Fig. 7). The pupal stage lasted 13

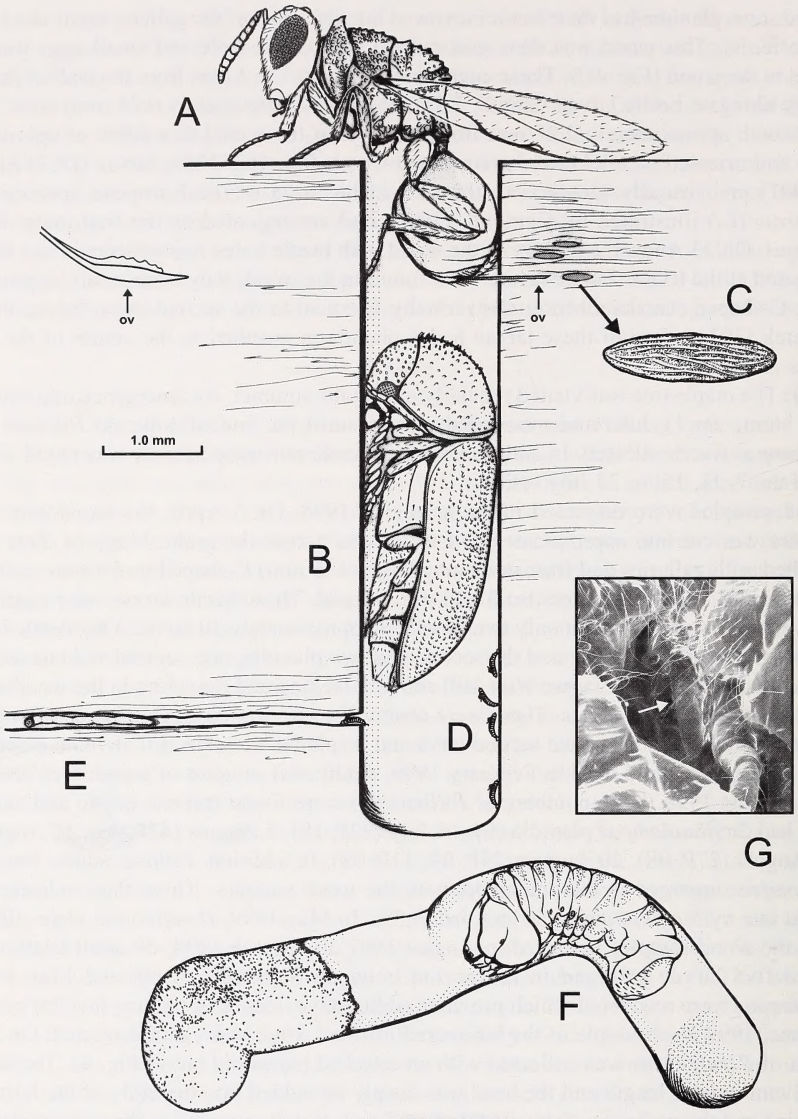


FIGURE 8. Diagrammatic representation of the interactions between *Steffanolampus salicetum* and its host, *Ptilinus ruficornis*. A. Female wasp in entrance hole, ovipositing into wood; ov, lateral view of apex of ovipositor. B. Dead female beetle passively blocking tunnel. C. Oviposition site and detail of *Steffanolampus* egg. Note: the weak ribbing of the chorion. D. Planidial first-instar larvae of *Steffanolampus* moving around in tunnel. E. First-instar beetle larva in wood. F. Final-instar beetle larva in gallery system with accumulated frass. G. SEM of planidium on venter of beetle larva. All illustrations except C and G to same scale.

days; the pupa was completely black on 8 July and the adult eclosed on 11 June. This rearing record provides incontrovertible documentation that *S. salicetum* is a primary parasitoid of *P. ruficornis*, and completes its development by feeding on the pupal stage of the host.

Figure 8 is a diagrammatic summary of various aspects of the life history of *S. salicetum* and its host *P. ruficornis,* based on field observations, laboratory dissections, and reasoned speculation based on published information on a European species of *Ptilinus* (Hickin 1963; Cymorek 1971). Primary attack is initiated when the mated female of *P. ruficornis* excavates an entrance tunnel across the grain of the wood. The females assume a "head out" orientation (B) and oviposit into the wood. The ovipositor length is approximately 2.4 mm (n = 4), which corresponds with the position that the first-instar larvae were found in the wood (E). Females die in the tunnels inhibiting the entry of predators and parasitoids. The beetle larvae begin feeding on the wood, moving randomly through the heartwood, and frass accumulates in the gallery system (F). After 5 or 6 instars, the larvae pupate and complete development. Females of *Steffanolampus* arrive on the wood after the beetle has initiated the entrance tunnels and continue to arrive after the females have died. The wasps walk backwards into available tunnels (A) and oviposit about 1 mm from the wall of the tunnel (C). This distance corresponds with the length of the ovipositor, which has strong teeth on the upper valve (A, ov). The planidia emerge from the egg and crawl back into the entrance tunnel (D), and apparently locate oviposition sites of the beetle, thereby gaining access to their hosts. The planidia attach to the beetle larva and remain on the exterior of the host (G), apparently reattaching at each successive moult. Feeding and subsequent development of the *Steffanolampus* planidium begins with host pupation.

Immature Stages of *Steffanolampus salicetum*

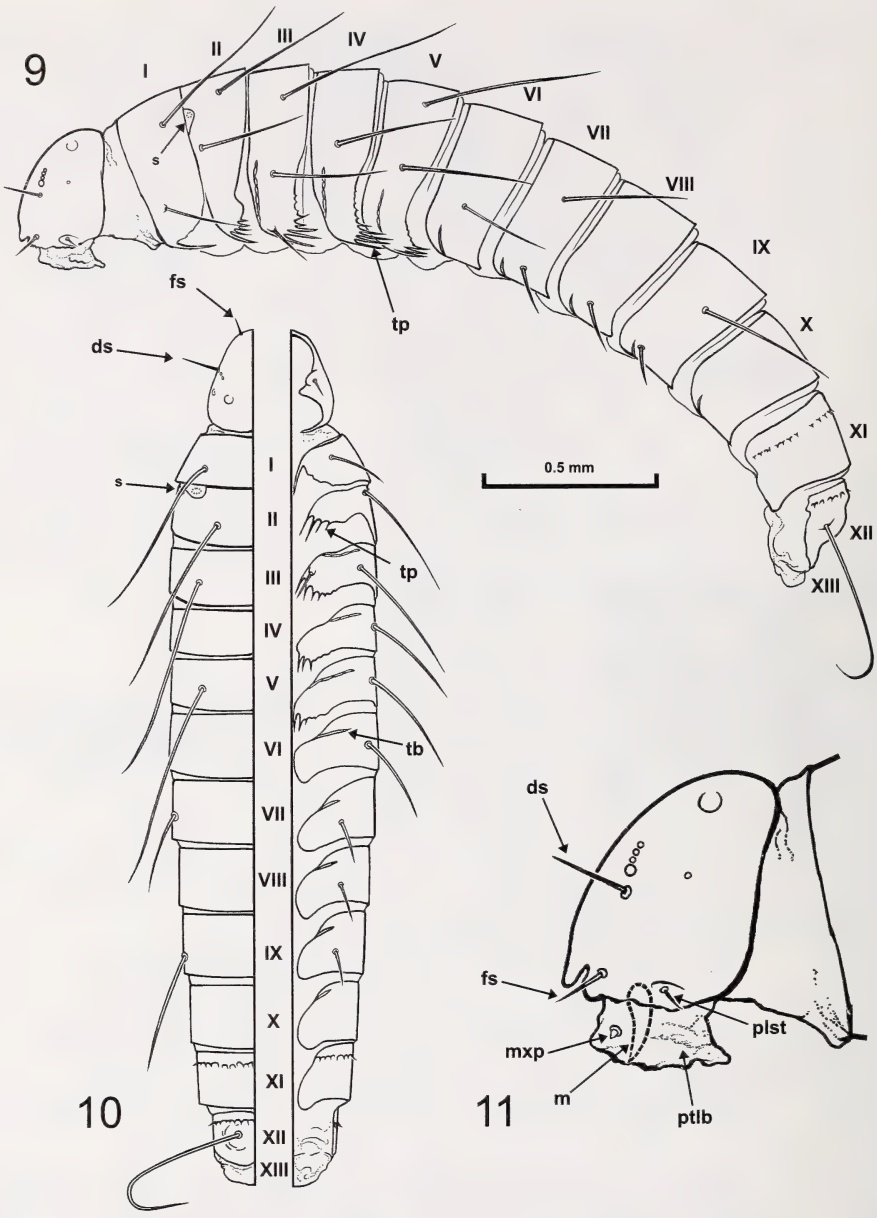
Ovarian Egg. Length approximately 0.42 mm, maximum width approximately 0.05 mm, fusiform and slightly curved, with chorion appearing lightly stippled (n = 10; DCD Slide No. 1981).

Deposited Egg (Fig. 8C). Length approximately 0.4 mm, maximum width approximately 0.1 mm, fusiform or spindle-shaped. Chorion weakly ribbed, evenly sculptured throughout (n = 5; DCD Slide Nos. 1982, 2047; DCD Photographs 1998-6, 10–19).

First-Instar Larva (Figs. 3, 8G, 9–11). Planidium, length approximately 0.2 mm, maximum width approximately 0.04 mm, cleared and slide-mounted specimens approximately 0.3 mm; fusiform, round in cross-section. Cranium and 13 body segments, I–XII sclerotized, yellow in color, XIII translucent, membraneous, forming a caudal pad or "sucker".

Cranium (Fig. 11) heavily sclerotized, with distinct hook on anterior margin; antenna absent, with three pairs of distinct cranial setae: forward-directed dorsal seta (ds) inserted in weak, circular depressions, backward-directed pleurostomal seta (plst), and forward-directed frontal seta (fs). Mandibles (m) large, symmetrical and sharply curved, bases broad and rounded. Labrum not distinctly differentiated. Postlabium (ptlb) well-developed, membraneous and extensible, with short, stout peg-like structures that may represent the maxillary palpi (mxp); with a bead-like row of 4 campaniform sensilla above the dorsal seta, the first clearly the largest, and a large circular depression dorsad.

Tergites I–XII heavily sclerotized, separated ventrad by membraneous areas (i.e., tergites do not completely encircle body), all tergites without tergopleural line. Spiracle(s) present dorsolaterad between tergites I and II, located beneath raised flap on tergite I . Tergites I and II apparently fused at least above the spiracle and separate only ventrad, not capable of telescoping; tergites III–XII separate, not fused, capable of telescoping. Setae all very long, longer than the width of their respective tergites; dorsal and lateral setae of I–V at least twice the width of tergites. Tergites I, II, V, VII, and IX with two pairs of setae, dorsal and lateral; tergites IV, VI, VIII with a single pair of lateral setae; tergite III with three pairs of setae, dorsal, lateral and ventral, the ventral pair not



FIGURES 9–11. First-instar larva of *Steffanolampus salicetum*. 9. Lateral habitus drawing. 10. Schematic representation of dorsal (left) and ventral (right) aspects showing shape of tergites and the position and length of the setae. 11. Lateral view of cranium and mouthparts. Abbreviations: ds, dorsal seta; fs, frontal seta; m, mandible; mxp, maxillary palp; plst, pleurostomal seta; ptlb, postlabium; s, spiracle; tb, tubercles; tp, tergal projections.

much smaller than the other setae; tergites X and XI without setae. Caudal cerci long and flexible, arising dorsad on tergite XII. Lateral margins of tergites I–V extended caudad as long needle-like projections (tp). Tergites VI–XI rounded ventrad, margin smooth without spines or serrations, XII extending only to lateral margin, not ventrad; with a row of triangular tubercles (tb) present on the ventral anteriod margin of III–X, serrations present in a similar position on XI but complete dorsal; serrations also present on XII.

Discussion

These field and laboratories studies clearly document that *S. salicetum* is a primary parasitoid of *P. ruficornis*. The phenological observations reported for *Ptilinus* at Joker's Hill are in accordance with the extensive data on flight activity, spatial and temporal distribution of the sexes as presented in Acciavatti (1972). His study, conducted in a similar forest type in upstate New York (Tully), reported a flight period of *P. ruficornis* from 10 June to 25 July. He also noted that the sex ratio of beetles emerging from infested wood was about 1:1 (302♂, 324♀), that there was a high preponderance of females observed on uninfested wood (35♂, 234♀), and that only females were found boring into the wood (229♀). *Steffanolampus* was not encountered in that study but there was a low level of parasitism by *Pelecotoma flavipes* Melsheimer (Coleoptera: Rhipiphoridae). In a study of dead maple trees in Ithaca, New York (Darling, unpublished) both *Steffanolampus* and *Pelecotoma* were collected together suggesting the possibility that *Steffanolampus* was a hyperparasite attacking *Pelecotoma.* The direct observations reported herein and the absence of the rhipiphorid from the Joker's Hill site confirm that *Steffanolampus* is a primary parasitoid of *Ptilinus.*

The oviposition sites and behaviour of female *Steffanolampus* are unique for the family Perilampidae. Their more precise oviposition behaviour explains the unwillingness of female *Steffanolampus* to oviposit in the lab. It is relatively easy to induce species of *Perilampus* and *Monacon* to oviposit under artificial situations simply by providing them with either plant material or damp filter paper. Pheromones are used in both the courtship (Hickin 1963) and aggregation of boring females (Acciavatti 1972) and these olfactory stimuli could be used by female *Steffanolampus* as kairomones to locate infestations of *Ptilinus.*

One of the fundamental differences between perilampids and eucharitids involves oviposition sites; eucharitids oviposit directly into plant tissue (Heraty 1997) whereas perilampids lay their eggs on leaves, flowers or stems (Perilampinae), or in preformed cavities in plant tissue (Chrysolampinae) (Darling 1997). The insertion of eggs into the wood by *Steffanolampus* females is eucharitid-like. This behaviour cannot be explained simply as a way of attacking xylophagous beetles feeding in concealed situations; *Monacon* species attack ambrosia beetles (Curculionidae: Platypodinae) but deposit eggs on the bark surrounding the entrance hole and it is the planidia that enter the tunnels, avoid the guarding behaviour of the males, and attach to the host beetle larva (Darling and Roberts 1999).

The planidium *S. salicetum* is virtually identical to those previously described for *Perilampus* and are very different from the planidium of *Monacon robertsi*, which is also a primary parasitoid of xylophagous beetles infesting the heartwood of dead or dying trees (Darling and Roberts, in press). The most distinctive feature of *Steffanolampus* planidia are the extremely long setae on the post-cranial segments; however, the distribution of dorsal, lateral and ventral setae conforms to the characterization of Perilampidae presented in Heraty and Darling (1984). Longer setae are present in *Perilampus* planidia that remain on the exterior of the host throughout their development, for example, *P. chrysopae* Crawford (Clancy 1946), but the setae of *Steffanolampus*, particularly those on the segments I–V, are at least twice as long as those described in any species of *Perilampus*. Another significant feature of these planidia is the dorsal fusion of tergites I and II;

these tergites are not fused in species of *Perilampus* studied to date (Heraty and Darling 1984). The fusion of these tergites could be a synapomorphy of *Steffanolampus*, *Krombeinius* (Darling 1995), and *Monacon* (Darling and Roberts, in press). Planidia are needed for additional species of *Perilampus* to test the generality of free tergites in this speciose and ecologically diverse genus. Fusion of tergites I and II is currently regarded as a synapomorphy of Eucharitinae (Heraty 1994), and free tergites are the groundplan state in Eucharitidae and Perilampidae. Fusion of these tergites has apparently occurred convergently in Eucharitinae and Perilampinae.

The behaviour of the planidia of *S. salicetum* is also similar to that of the strictly ectoparasitic planidia of *Perilampus* and *Monacon*, e.g., *P. chrysopae* Crawford (see Clancy 1946) and *M. robertsi* (Darling and Roberts 1999). These planidia never enter the haemocoel of the host but remain external and apparently transfer from the shed exuvium to the next larval instar of the host at each successive moult. Most species of *Perilampus* studied are hyperparasitoids, attacking hymenopteran (Ichneumonidae and Braconidae) and dipteran (Tachinidae) parasitoids of Lepidoptera (see Laing and Heraty 1981 for a local example of this life history, *P. fulvicornis* Ashmead). These planidia enter the haemocoel of their ultimate host and emerge to begin feeding as an ectoparasite when the host pupates. Planidia that enter the haemocoel of the host have stouter recurved hooks on the head presumably to facilitate penetration of the host haemocoel (e.g., *P. tristis* Mayr, Bergold and Ripper 1937; *P. hyalinus* Say, Tripp 1962). These spines are probably homologous to the dorsal and cranial setae of strict ectoparasitoids like *S. salicetum.*

The subsequent larval instars of *S. salicetum,* although not studied in detail, are consistent with those reported for other perilampine genera. Of note is the feeding position of the second-instar, which is imbedded into the host as reported for the third-instar of *M. robertsi* Bouček (see fig. 2d in Darling and Roberts 1999). This feeding position may be a result of limited space in the gallery system for both the host and parasitoid. The lateral protuberances of the third-instar larva of *Steffanolampus* are similar to those reported and illustrated in *Perilampus* (e.g., *P. tristis*, Bergold and Ripper 1937; *P. chrysopae*, Clancy 1946; *P. hyalinus*, Tripp 1962).

There seems to be very little potential of *S. salicetum* as a biological control agent for *P. ruficornis* and other destructive anobiid beetles. Xylophagous anobiids not only attack dead and dying trees but are also serious pests of wood products (Craighead 1950), such as sawlogs and cordwood, flooring, woodwork, structural timbers and furniture (Acciavatti 1972). The low levels of parasitism found in even large aggregations of anobiid hosts suggests that other biological control agents would be more effective. Parasitoids are not overly effective in controlling infestations of most xylophagous beetles that feed in heartwood (cf. cambium feeders like bark beetles). A recent case in point is the newly introduced Asian longhorned beetle for which fungal pathogens are thought to offer the best biological control possibilities (Richard Hoebeke, pers. comm.). *Steffanolampus salicetum* does, however, exhibit interesting behaviours and a complex life cycle that is closely coordinated with that of its hosts and are therefore worthy of study in their own right.

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GEOMYZA TRIPUNCTATA FALLÉN, A PALAEARCTIC OPOMYZID FLY NEW TO NORTH AMERICA, WITH NOTES ON RANGE EXPANSIONS IN HOLARCTIC OPOMYZIDAE (DIPTERA)

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Abstract *Proc. ent. Soc. Ont.* 130: 15–20

The western Palaearctic opomyzid fly *Geomyza tripunctata* Fallén is recorded from the Nearctic region for the first time, from specimens collected in Ontario, Quebec, Nova Scotia and Prince Edward Island. The species was probably introduced to eastern Canada by human activity. The date of the initial introduction is unknown, but the range expansion of *G. tripunctata* in southern Ontario is quite recent, probably since the mid 1980s, and the species appears to be expanding its range rapidly in that region. *Geomyza tripunctata* is illustrated and distinguished from the ten other known Nearctic species of *Geomyza*. Notes on range expansions in the Nearctic region are also provided for two other Holarctic species of Opomyzidae, *Opomyza germinationis* (L.) and *O. petrei* Mesnil.

Résumé *Proc. ent. Soc. Ont.* 130: 15–20

Geomyza tripunctata Fallén, un opomyzid paléarctique a été découvert pour la première fois dans la région néarctique. Les spécimens ont été collectés en Ontario, Québec, Nouvelle Écosse, et à l'Île du Prince Édouard. Cette espèce a problement été introduite dans l'est du Canada par l'intermédiaire des activités humaines. La date de cette introduction n'est pas connue, mais la présence de *G. tripunctata* en Ontario est récente, probablement depuis le milieu des années quatre-vingts et l'espèce semble étendre sa distribution rapidement dans cette région. Ici, *G. tripunctata* est différentiée des dix autres espèces néarctiques connues de *Geomyza*. De plus, la nouvelle répartition plus étendue dans la région néarctique de deux autres espèces holarctiques d'Opomyzidae, *Opomyza germinationis* (L.) et *O. petrei* Mesnil est donnée.

Introduction

It is clear that there are more species of Holarctic acalyptrate Diptera than previously realized. Many species have been recorded as either naturally Holarctic, or introduced from the Palaearctic region (e.g., McAlpine 1965; Hoebeke and Wheeler 1994; Wheeler 1994). With more effort to document such range extensions by collecting in likely localities, the number of Holarctic species will probably continue to rise. The Opomyzidae is one family in which there are already several known Holarctic species; five of 13 species known from the Nearctic region are either

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naturally Holarctic or have been introduced to North America. *Opomyza germinationis* (L.) and *O. petrei* Mesnil were introduced to the east and west coasts of North America, respectively, and *Geomyza balachowskyi* Mesnil was introduced to both the east and west coasts (Vockeroth 1961). Vockeroth (1961) considered *Anomalochaeta guttipennis* (Zetterstedt) and *Geomyza apicalis* (Meigen) naturally Holarctic. We have been aware for some time of another Palaearctic species of *Geomyza* in eastern North America; the purpose of this paper is to record the presence of *Geomyza tripunctata* Fallén in the Nearctic region, and to provide notes on range expansions of *G. tripunctata* and other Holarctic Opomyzidae based on collections made since Vockeroth (1961).

Materials and Methods

The specimens on which this paper is based are housed in the following collections (acronyms used in the text are in parentheses): Canadian National Collection of Insects, Ottawa, ON (CNC); University of Guelph Insect Collection, Guelph, ON (GUE); collection of K.N. Barber, Sault Ste. Marie, ON (KNB); Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC (LEM).

Preparations of postabdomens were made by removing abdomens from specimens and clearing them for several minutes in warm 85% lactic acid. Cleared abdomens were placed in glycerin for further dissection and examination.

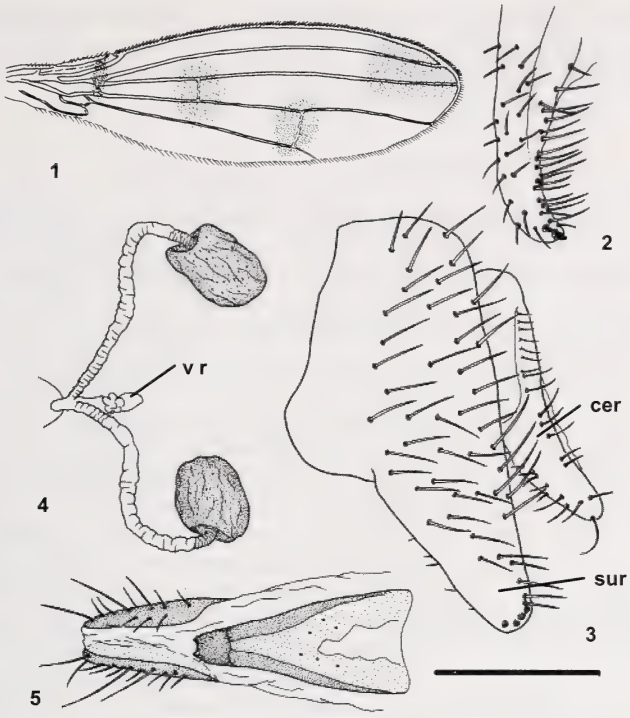
Results

Geomyza tripunctata Fallén

Diagnosis. *Geomyza tripunctata* may be distinguished from all other known *Geomyza* species in the Nearctic region by the wing pattern, with a distinct, large spot at the apex and one large spot over each of crossveins r-m and dm-cu (Fig. 1). The wing pattern permits identification of this species in the field, without the need for magnification. *Geomyza tripunctata* also has a strong anepimeral bristle (pteropleural bristle of Vockeroth, 1961), a character present only in *G. lurida* (Loew) among the other Nearctic species of the genus. *Geomyza lurida* is known only from west of the coastal mountain ranges from Alaska to California and has much smaller spots on the crossveins than does *G. tripunctata* (see fig. 4 in Vockeroth, 1961).

Mesnil (1934) and Balachowsky and Mesnil (1935) provided comprehensive descriptions and illustrations of external characters for *G. tripunctata*. Illustrations of the male and female genitalia are included here. The male genitalia are relatively uniform in *Geomyza*, with only minor differences in shape of the epandrium, surstylus and cercus among species. The surstylus of *G. tripunctata* is straight and evenly tapering, with a broadly rounded apex (Fig. 3), which is slightly curved medially, and has a single row of 4–7 short stout subapical spines on the medial surface (Figs. 2–3). The cercus is slightly curved posteriorly with scattered fine setae apically (Fig. 3). The female sternite 8, cerci, spermathecae and ventral receptacle of *G. tripunctata* are illustrated in Figs. 4–5. The female genitalia of most other Nearctic species of *Geomyza* have not been illustrated, but may provide useful taxonomic characters.

Specimens examined. CANADA: **Nova Scotia**: 1km N Mabou, picnic area beside highway, 16.viii.1996, T.A. Wheeler and S. Boucher, sweeping disturbed grasses and herbage (1♂, 1♀, LEM); **Ontario**: Almonte, Indian River, 29.v.1992, T.A. Wheeler, swept along shore (1♀, LEM); Burlington, edge Tuck Ck, 20.vii.1997, K.N. Barber, sweeps/pooter *Bromus inermis*, 43°21.2'N, 79°46.6'W (1♂, 1♀, KNB); Fergus, Grand R., floodplain, 17.vii.1997, K.N. Barber, sweeps/pooter, *Phalaris arundinacea*, 43°41.5'N, 80°23.2'W (1♂, 1♀, KNB); same data except sweeps/pooter,



FIGURES 1–5. *Geomyza tripunctata*: 1, wing; 2, male left surstylus, posterior; 3, male epandrial complex, left lateral; 4, female spermathecae and ventral receptacle; 5, female sternite 8 and cerci, ventral. Abbreviations: cer - cercus; sur - surstylus; vr - ventral receptacle. Scale bar (Figures 2–5) = 0.2 mm.

Bromus inermis (2♂, 5♀, KNB); Fergus, on *Formica* mound, 07.iv.1996, S.A. Marshall (2♀, GUE); Ottawa, 06.vi.1987, J.R. Vockeroth (1♂, 1♀, CNC); same data except 12.v.1987 (1♀, CNC); Ottawa, 15.viii.1987, J.R. Vockeroth, swept from *Sagittaria* (1♀, CNC); Ottawa, 04.vii.1989, J.R. Vockeroth, swept over bare path in *Acer* wood (1♀, CNC); Ottawa, 18.vii.1990, J.R. Vockeroth, damp second growth *Acer-Betula* wood (1♂, CNC); same data except 23.vii.1990 (1♀, CNC); same data except 27.iv.1991 (1♀, CNC); same data except 22.vii.1991 (1♀, CNC); Ottawa, nr. Uplands Airport, 22.v.1990, J.M. Cumming (1♀, CNC); ca. 1km NW Ponsonby, 17.vii.1997, K.N. Barber, sweeps/pooter, roadside, mostly *Poa pratensis* and *Poa compressa*, 43°38.2'N, 80°22.9'W (5♂, 4♀, KNB); **Prince Edward Island**: 1km SW Suffolk, sweep grasses along roadside, 15.viii.1996, T.A. Wheeler and S. Boucher (1♂, 1♀, LEM); **Quebec**: Lachute, 08.ix.1992, J.R. Vockeroth, swept in *Acer-Tsuga* wood (1♂, CNC); Old Chelsea, 20.v.1987, J.R. Vockeroth (1♂, CNC); Luskville, Piton Rd., 19.iv.1993, J.R. Vockeroth (1♀, CNC); Lac Roddick, 12 km N Bouchette, 10.x.1999, L. Masner, pan trap on lakeshore (1♀, CNC); Ste-Anne-de-Bellevue, Morgan Arboretum, vi.1995, C. Riley, pan traps in *Typha* at pond margin (1♀, LEM); Ste-Anne-de-Bellevue, Stoneycroft (45°25.8'N, 73°56.4'W), sweep grass at south end of pond, 28.v.1998, J. Savage (1♀, LEM); same data except 02.vii.1998 (1♂, 4♀, LEM); same data except 02.vii.1998, J. Pérusse

(1♀, LEM); Ste-Anne-de-Bellevue, Stoneycroft (45°25.8'N, 73°56.4'W), sweep vegetation near pond, 02.vii.1999, T.A. Wheeler (1♀, LEM).

Distribution. Palaearctic region: widespread throughout Europe (Soós 1984). Nearctic region: southern Ontario, southwestern Quebec, Prince Edward Island, Nova Scotia.

Opomyza germinationis (L.)

Vockeroth (1961) recorded this species from a single female specimen collected in 1958 at Lockeport, Nova Scotia. We have identified over 40 specimens collected between 1983 and 1996 in Nova Scotia and Newfoundland and the species is clearly established in eastern North America. *Opomyza germinationis* was apparently introduced to eastern Canada from Europe.

Specimens examined. CANADA: **Newfoundland**: St. John's, window bldg 810, 06.vii.1983, L. Hollett (1♂, CNC); St. John's, grassy area, 05.ix.1983, L. Hollett (1♀, CNC); Portugal Cove, sweep pasture, 01.vii.1987, T.A. Wheeler (2♀, GUE); same data except 07.vii.1987 (1♂, GUE); same data except 11.vii.1987 (3♂, 3♀, GUE); Portugal Cove, at light, 11.vii.1987, T.A. Wheeler (1♂, 2♀, GUE); **Nova Scotia**: Cape Breton Highlands Nat. Pk., Pleasant Bay, 25–29.vi.1984, H.J. Teskey, dry mixed forest (4♂, 4♀, CNC); same data except 2–11.vii.1984 (2♂, 1♀, CNC); same data except 28.vi.1984 (1♂, 1♀, CNC); same data except 10.vii.1984 (1♂, 2♀, CNC); Cape Breton Highlands Nat. Pk., South Harbour, 9.vii.1983, J.R. Vockeroth, mixed dry mesophytic woods (1♂, CNC); Cape Breton Highlands Nat. Pk., South Harbour, 27.vi.1983, J.R. Vockeroth, marshy lake shore, brackish water, *Carex, Iris, Juncus* (2♀, CNC); Cape Breton Highlands Nat. Pk., Beulach Ban Falls, 11.vii.1983, J.R. Vockeroth, swept along fast rocky stream (1♀, CNC); Lockeport, 20.vii.1958, J.R. Vockeroth (1♀, CNC); Antigonish, 18.vi.1983, J.E. Corrigan (2♂, 2♀, GUE); Little Bras D'or, 03–04.viii.1992, J. Skevington and A. Goering, malaise, field (1♂, 1♀, GUE); 1km N Mabou, picnic area beside highway, 16.viii.1996, T.A. Wheeler and S. Boucher, sweeping disturbed grasses and herbage (2♂, 2♀, LEM).

Opomyza petrei Mesnil

Vockeroth (1961) recorded this species from several localities in southwestern British Columbia and on Vancouver Island. Like *O. germinationis,* this species is apparently introduced. *Opomyza petrei* has recently been collected in eastern Canada as well, suggesting that it, like *Geomyza balachowskyi*, has been introduced on both the east and west coasts of North America. The single specimen from Ohio, collected far inland, may be evidence of further dispersal of introduced coastal populations, especially because the locality is close to Lake Erie and heavy shipping traffic. The presence of the species in Ohio could also indicate that the species is naturally Holarctic, as suggested for *Geomyza apicalis* by Vockeroth (1961) and the chloropid fly *Conioscinella zetterstedti* Andersson by Wheeler (1994). This latter explanation would be more plausible, however, if more than a single specimen had been collected in inland localities, and if eastern Nearctic specimens had been collected before 1962.

Specimens examined. (22 specimens listed by Vockeroth (1961) omitted). **CANADA**: **British Columbia**: Pitt Meadow, 16.vi.1960, A.T. Wilkinson (1♂, 1♀, CNC); Royal Oak, 15.vii.1959, L.A. Kelton (1♂, 1♀, CNC); Vancouver, UBC campus, forest trail, 3–9.vii.1988, S.A. Marshall (1♀, GUE); **Nova Scotia**: Ingonish, North Bay, 7–8.vii.1984, H.J. Teskey (1♂, CNC); Cherry Hill, 20.viii.1989, along shore, S.A. Marshall (1♂, GUE); 1km N Mabou, picnic area beside highway, 16.viii.1996, T.A. Wheeler and S. Boucher, sweeping disturbed grasses and herbage (3♂, 4♀, LEM). **USA**: **Ohio**: Mimisla Lake, 16.viii.1962, D. Miletich (1♂, CNC); **Oregon**: Benton Co.,

Lobster Valley, 15mi SW Alsea, 27.v.1975, J.D. Lattin (1♂, 1♀, GUE); **Washington**: Olympia, 23.vii.1960, F.C. Harmston (1♂, CNC); Quinault, 21.vii.1960, F.C. Harmston (1♀, CNC).

Discussion

Vockeroth (1961) predicted that *Geomyza tripunctata*, a common species in the western Palaearctic, would eventually be recorded in North America. It is difficult to reconstruct the history of the introduction and subsequent movements of *G. tripunctata* in eastern Canada, mainly because of collection bias. While the Diptera fauna of regions surrounding Ottawa and Guelph has been subject to regular collecting in recent decades, this is not true of Quebec and the Atlantic provinces, where interest in small acalyptrate Diptera has been less pronounced. The first known Nearctic specimens of *G. tripunctata* were collected in 1987 and all specimens collected before 1992 were taken in the Ottawa region. *Geomyza tripunctata* was probably not established in the Ottawa region before the 1980s because the Diptera of that region have been well collected for many years and it is unlikely that such a conspicuous species would have been overlooked. Given the broad geographic distribution of specimens collected since 1996, *G. tripunctata* seems to be expanding its range rapidly in southern Ontario. Extensive collecting has been done by students and staff at the University of Guelph since the mid 1970s and it is unlikely that *G. tripunctata* was established in southwestern Ontario much before the first collections there in 1996. Since 1996, we have made a more concerted effort to collect this species east of Ottawa, and it has now been recorded in several localities and is clearly widespread in eastern Canada. The lack of past collecting of acalyptrate Diptera in Quebec and the Atlantic provinces makes it impossible to determine whether *G. tripunctata* has been established in eastern Canada for some time or whether specimens from there represent a recent range expansion.

An unresolved question concerning the Holarctic species of Opomyzidae (and other families) is the origin of the Nearctic fauna. Despite strong circumstantial evidence for recent introduction, it is impossible to establish, based on morphological and geographic criteria, whether Nearctic populations of Holarctic species such as those discussed here are naturally Holarctic or recently introduced (and if so, on how many occasions). Analysis of population level genetic characters may provide the necessary evidence to establish the approximate time of divergence of Nearctic and Palaearctic populations of these species. Efforts should also be made to determine the actual distribution of such species in the Nearctic. While established insect collections provide crucial data on the introduction and range expansion of species, those data are often limited by a lack of collecting in appropriate regions. Continued faunal inventories are necessary to document the changing distributions of insect species.

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WORLD REVIEW OF THE *CAMPTOPTERA* GROUP OF GENERA (HYMENOPTERA: MYMARIDAE)

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Abstract *Proc. ent. Soc. Ont.* 130: 21–65

The group of genera related to *Camptoptera* Förster is re-defined and five other genera are recognized: *Callodicopus* Ogloblin, *Camptopteroides* Viggiani, *Eofoersteria* Mathot, *Macrocamptoptera* Girault, and *Stephanocampta* Mathot. *Eomymar* Perkins, **syn. nov.**, is synonymized under *Camptoptera* and a lectotype is designated for its type species, *Eomymar muiri* Perkins. *E. maximus* Girault is transferred to *Mimalaptus* as *M. maximus* (Girault), **comb. nov.** *Paranagroidea* Noyes and Valentine, **syn. nov.**, is synomymized under *Camptopteroides* and its only described species is transferred to *Camptopteroides* as *C. verrucosa* (Noyes and Valentine), **comb. nov.** *Macrocamptoptera* is removed from synonymy under *Camptoptera* and its generic status re-established. *Herulia* Hedqvist, **syn. nov.**, and *Rhila* Donev, **syn. nov.**, are synomymized under *Macrocamptoptera* and their included species are transferred to *Macrocamptoptera* as *M. sundholmi* (Hedqvist), **comb. nov.** and *M. bulgarica* (Donev), **comb. nov.**, respectively. *Hadromymar* Yoshimoto, **syn. nov.**, is synonymized under *Stephanocampta* Mathot and its only described species is transferred to *Stephanocampta* as *S. masoni* Yoshimoto, **comb. nov.** *Staneria,* **syn. nov.**, is synonymized under *Camptoptera* and its only described species is transferred to *Camptoptera* as *C. diademata*, **comb. nov.** *Decamymar* Annecke, **syn. nov.**, is synonymized under *Callodicopus* and its only described species is transferred to *Callodicopus* as *C. magniclavae* (Annecke), **comb. nov.** *Camptoptera vasta* Girault is transferred to *Eofoersteria* as *E. vasta* (Girault), **comb. nov.** *Sphegilla franciscae* Debauche, *S. japonica* Taguchi, and *Wetanekiella brevicornis* Soyka are transferred to *Camptoptera* as *C. franciscae* (Debauche), **comb. nov.**, *C. japonica* (Taguchi), **comb. nov.** and *C.* **brevicornis** (Soyka), **comb. nov.**, respectively. A new subgenus, *Alalinda* Huber **subgen. nov.**, of *Camptopteroides* and two new species are described: *C.* (*Camptopteroides*) *alata* Lin from China and *C.* (*Alalinda*) *dorothea* Huber from North America.

Introduction

The worldwide mymarid genus *Camptoptera* Förster (1856) is one of about 13 classical genera of Mymaridae (those described before 1900, excluding currently recognized synonyms). The number of genera proposed up to the end of 1999 currently is 175, but with synonymy over the years this has been reduced to 104 recognized genera. Since Annecke and Doutt (1961) proposed the last formal classification of Mymaridae, dividing it into five tribes in two subfamilies, the tendency

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has been not to classify the genera at all because the tribes and subfamilies are most likely polyphyletic. Viggiani (1989) presented a considerably different grouping of the family based solely on male genitalia. Clearly, much work remains to be done to sort out generic limits properly and work out generic relationships more fully before a robust higher classification can finally be developed.

Camptoptera is the most speciose genus in a group of 13 nominal genera that we call the *Camptoptera* group. This informal generic grouping was proposed initially by Soyka (1961) but we define it more broadly based on examination of many more nominal genera than he did. We recognize six genera in the group and synonymize seven others. The features that different authors proposed to define their grouping of *Camptoptera* and related genera, or to permit their separation from other groups, vary. Until a detailed comparison of the same suite of characters across all the genera worldwide is made we consider it premature to accept a formal classification such as the Camptopterinae of Viggiani (1989). Such a classification should be based on well-founded apomorphies defining monophyletic groups, where possible. The *Camptoptera* group is likely monophyletic but single apomorphic characters or groups of characters have not yet been found that demonstrate this conclusively. The emphasis of this paper is, therefore, to clarify the genera within the group rather than demonstrate the monophyly of the entire group. This can only be done once related groups of genera are studied in more detail and character polarities determined with greater confidence. We discuss each genus of the *Camptoptera* group, update geographic distributions of the genera based mainly on specimens in the Canadian National Collection of Insects, describe a new subgenus and two new species of *Camptopteroides*, and provide a generic key.

Historical Summary

Over 50 years after *Camptoptera* was described two other related genera, *Macrocamptoptera* Girault (1910) and *Eomymar* Perkins (1912) from North America and Asia, respectively, were described. *Eofoersteria* Mathot (1966), *Stephanocampta* Mathot (1966), *Camptopteroides* Viggiani (1974), *Decamymar* Annecke (1961), *Staneria* Mathot (1966), *Paranagroidea* Noyes and Valentine (1989), *Hadromymar* Yoshimoto (1990), and *Rhila* Donev (1989) were described more recently but several of these names are synonymized below. Ogloblin (1955) proposed four new genera related to *Dicopus* and suggested that these should be placed in their own tribe. We add one of these genera, *Callodicopus*, to the *Camptoptera* group; the remaining genera belong in the *Alaptus* group, discussed briefly below.

Soyka (1961) included four genera in his "*Camptoptera* group": *Camptoptera, Stichothrix* Förster, *Macrocamptoptera*, and *Wertanekiella* Soyka. Annecke and Doutt (1961) classified three genera, *Sphegilla*, *Camptoptera* and *Eomymar*, in their tribe Ooctonini together with several other genera that are here considered to be not closely related to these. In his cladistic analysis of Holarctic genera, Schauff (1984: 25) included five genera, *Camptoptera, Sphegilla, Litus, Alaptus* and *Dicopus*, in his informal *Alaptus* group of genera but he deliberately did not propose a subfamily classification. We would modify his *Alaptus* group to exclude *Camptoptera* and probably also *Litus*. Based on their study of the New Zealand fauna, Noyes and Valentine (1989) proposed another informal group, "subgroup a" of their *Anaphes* group, included two genera in it, *Camptoptera* and *Paranagroidea*, and also deliberately omitted a formal subfamily classification. In a preliminary classification of subfamilies and tribes, Viggiani (1989) proposed the subfamily Camptopterinae and placed *Camptoptera* and *Camptopteroides* in it. None of these authors examined or included in their classifications more than three genera besides *Camptoptera*, usually because their work was regional. In Viggiani's (1989) case the classification proposed was based strictly on male genitalia.

Materials and Methods

Representatives of most of the genera discussed below are in the Canadian National Collection of Insects, Ottawa (CNCI). Material was also examined from the following collections:

ANIC Australian National Insect Collection. J. Cardale
BPBM Bishop Museum, Honolulu, USA. G. Nishida
FAU Biological Control Research Institute, Fujian Agricultural University, Fuzhou, China. Lin N.-Q.
QMBA Queensland Museum, Brisbane, Australia. C. Burwell
SANC South African National Collection of Insects. G. Prinsloo
UCDC University of California, Davis. S. Heydon
UCRC University of California, Riverside. S. Triapitsyn
UPPH University of Plovdiv "P. Hilendarski", Plovdiv, Bulgaria. A. Donev

Measurements were made from slide mounted specimens except for body length, which was from card or point mounted specimens. *Camptopteroides alata*, **sp. nov.**, measurements were made at 200X and 400X magnification; measurements of *C.* (*Alalinda*) *dorothea* **sp. nov.** were made at 125X and 250X magnification. Body length is measured from anterior margin of head to apex of metasoma, excluding the exserted part of the ovipositor. The diagnoses for each genus are compared only to other genera within the *Camptoptera* group. Distributions are based mainly on specimens in the CNCI. Unlike most mymarids, sexual dimorphism in forewing shape occurs in *Camptopteroides* (Figs. 1,2). Like all other Mymaridae, sexual dimorphism in antennae is pronounced (Figs. 4, 5)

The number and position of body setae are fairly constant and usually bilaterally symmetrical for a given species or genus. The descriptions in this paper follow the format for setae given in Annecke and Doutt (1961). For example, "1 and 1 setae between posterior ocelli", refers to the single setae on each side of the midline that occurs between the posterior ocelli (e.g., Fig. 3). The abbreviation F stands for funicular segment (females) or flagellar segment (males). Terms used for the male genitalia (Fig. 6) follow Gibson (1997).

Specimens of at least one species of each genus except *Eofoersteria*, where there was insufficient material available, were prepared for scanning electron microscopy (SEM) following Bolte (1996). Microscope slides of wings were photographed with a digital camera. The SEM micrograph negatives were scanned into a computer with a 35 mm scanner. All micrographs and wing images were digitized, enhanced, and the final plates compiled and labelled electronically. In order to facilitate comparison among genera the SEMs and photographs are organized by structure, as follows: head (Figs. 7–42), mesosoma (Figs. 43–78), metasoma (Figs. 79–106), wings (Figs. 107–116), and antennae (Figs. 117–127).

The *Camptoptera* group of genera

As constituted here, the *Camptoptera* group is most closely related to the *Alaptus* group of genera, which includes *Alaptus*, *Dicopomorpha*, *Dicopus*, *Kubja*, *Mimalaptus* and perhaps others. Before listing the combination of features that define the *Camptoptera* group we list the principal distinguishing features of the *Alaptus* group:

1. very broad junction of mesosoma to metasoma with little indication of a narrowing between mesosoma and metasoma.
2. mesophragma projecting far into the metasoma.
3. lack of a vertical median groove above the foramen magnum (except *Dicopus*).

4. scutellum short and distinctly divided by a transverse groove into anterior and posterior portions of about equal length.
5. first gastral tergum similar in length and shape (along posterior margin) to the remaining terga.

The combination of 10 features that defines the *Camptoptera* group is listed below. No single feature can be used that unequivocally includes all members of the group and excludes all members outside the group. Thus, within the group there is at least one genus that lacks a particular feature and outside the group there is at least one genus that has that particular feature. Nevertheless, the *Camptoptera* group can be defined reasonably well as follows: Occiput sharply margined at vertex, and with either a vertical median groove or a transverse groove or both above foramen; scutellum entire, not divided by transverse suture; petiole usually distinct, narrow but at most only slightly longer than broad. *Camptoptera*-group species are relatively gracile compared to the short, stocky members of the related *Alaptus* group of genera. With experience and practice, members of the group can usually be recognized by their habitus.

1. Occiput divided by either vertical or horizontal grooves, or both, above the foramen. A median, vertical groove occurs above the foramen (Figs. 17, 23, 35, 41), in all the genera except some *Camptopteroides* (Fig. 11) and *Stephanocampta* (Fig. 29). A transverse, curved or angled groove or thickening that is complete or incomplete just above foramen (Figs. 11, 17, 29, 35, 41), occurs in all the genera except *Macrocamptoptera* (Fig. 23). *Dicopus* has a vertical groove.
2. Junction between vertex and occiput sharply defined (Figs. 11, 17, 23, 29, 35, 41), with the occiput flat or slightly concave (Figs. 8, 14, 20, 26, 32, 38).
3. Mandibles with either 1 tooth in *Camptoptera* (Fig. 36), *Eofoersteria*, and *Stephanocampta* (Fig. 30) or 2 teeth in *Camptopteroides* (Figs. 12, 18), *Macrocamptoptera* (Fig. 24), and *Callodicopus* (Fig. 42).
4. Female either with 6 funicular segments [in *Eofoersteria* (Fig. 127), some *Camptoptera* (Fig. 124) and some *Camptopteroides* (Fig. 119)] or 7 funicular segments. In species with 7 funicular segments, F2 is usually wider than long, i.e., ring-like (Figs. 4, 117, 118, 120, 121, 123, 126), except in a few *Camptoptera*, some *Stephanocampta* (Fig. 122), and *Callodicopus* (Fig. 125) where it is longer than wide.
5. Male with 10 flagellomeres [only 7 in the two species formerly placed in C. (*Zemicamptoptera*)], of which F2 (Fig. 5) and sometimes also F4 are ring-like. Males of *Eofoersteria* and species formerly placed in *Sphegilla* are unknown but when found it is expected that they will have at most only 9 flagellomeres.
6. Anterior portion of scutellum separated from distinctly longer posterior portion by a transverse row of fovea, curved in *Camptopteroides* (Figs. 43, 49) and straight in *Macrocamptoptera* (Fig. 55) or a fine incomplete line in *Stephanocampta* (Fig. 61) or without a separation in *Camptoptera* (Fig. 67), *Callodicopus* (Fig. 73), and *Eofoersteria*.
7. Forewing of macropterous forms narrow, with the longest fringe setae much longer than greatest wing width (Figs. 1, 3, 107, 109–113), and often with posterior margin towards the apex distinctly concave so the wing appears curved apically (posterior margin straight or almost so in macropterous *Camptopteroides*, Figs. 107, 109). In brachypterous *Camptopteroides* (Fig. 108) the marginal fringe is greatly reduced and the wing appears to be relatively wider.
8. Gaster usually strongly constricted basally and with a narrow petiole not more than about twice as long as wide (Figs. 91–105), and with mesophragma not projecting into gaster, except

in *Callodicopus*, which has the mesophragma projecting through the broad, ring-like and indistinct petiole into the gaster (Fig. 106).

9. First gastral tergum often distinctly longer than following terga and with its posterior margin cleft, serrate or undulate.
10. Ovipositor short and originating beyond middle of gaster (Figs. 80, 84, 86–90), except in *Camptopteroides* (*Alalinda*) where it is longer than half gaster length (Fig. 82).

The genera *Callodicopus*, in the *Camptoptera* group, and *Mimalaptus* Noyes & Valentine, in the *Alaptus* group, appear superficially to be annectant between the two groups of genera. *Callodicopus* species have the structure of the head, scutellum, and first gastral tergum typical of other *Camptoptera*-group genera but have the relatively broad junction between mesosoma and metasoma with a very reduced, indistinguishable petiole similar to *Alaptus*-group genera. On the balance of features, *Callodicopus* is best placed in the *Camptoptera* group. *Mimalaptus* species also appear to share features between the two groups, in particular the curved forewing. However, most features clearly show that *Mimalaptus* belongs in the *Alaptus* group. *Mimalaptus* species have little indication of a constriction between mesosoma and metasoma and they have the apomorphic scutellar structure similar to *Alaptus*. Thus we concur with Noyes and Valentine's (1989) placement of *Mimalaptus* near *Alaptus* and *Dicopus*.

The remaining five genera of the *Camptoptera* group can be divided into two subgroups based on the presence of either 1 or 2 mandibular teeth, and the other features mentioned in key couplet 2. *Macrocamptoptera* and *Camptopteroides* form one subgroup, and *Camptoptera*, *Stephanocampta*, and *Eofoersteria* form the other.

Key to *Camptoptera*-group genera

1 Propodeal foramen large, laterally almost touching each metacoxal foramen (Fig. 106); metasoma apparently without petiole and mesophragma projecting into gaster (Fig. 106) .... *Callodicopus* Ogloblin

– Propodeal foramen small, well separated from each metacoxal foramen; metasoma with distinct but sometimes very short gastral petiole (Figs. 91–105) and the mesophragma not projecting past posterior margin of propodeum 2

2(1) Mandibles with 2 teeth (Figs. 12, 18, 24); forewing beyond venation usually with more or less distinct dark areas (Figs. 107–110); head and propodeum with heavy, reticulate sculpture (Figs. 2, 7–24, 43–60); procoxae widely separated anteriorly by broad anterior apex of prosternum (Figs. 45–47, 51–53, 57–59); scutellum with curved, transverse row of fovea separating anterior from posterior portions (Figs. 43, 49, 55) 3

– Mandibles with 1 tooth (Figs. 30, 36); forewing beyond venation at most with only faint, uniform, darker suffusion (Figs. 111–113, 114); head and mesosoma with inconspicuous sculpture (Figs. 25–36, 61–72); procoxae almost abutting or slightly overlapping anteriorly, the anterior apex of prosternum pointed (Figs. 63–65, 69–71); scutellum without row of fovea separating anterior from posterior portions (Figs. 61, 67) 4

3(2) Forewing with long, distinct macrochaetae, especially the distal macrochaeta (Figs. 107–109); head with moderately long setae on face and vertex (Figs. 2, 7–17); occiput with at least a short, curved or angled, transverse groove above foramen (Figs. 11, 17); prosternum anteriorly with parallel lateral margins (Figs. 45, 46, 51, 52) ..... *Camptopteroides* Viggiani

– Forewing with very short, inconspicuous macrochaetae (Fig. 110); head with very short, indistinct setae (Fig. 19–24); occiput without horizontal groove above foramen (Fig. 23); prosternum anteriorly with diverging lateral margins (Fig. 57) ... *Macrocamptoptera* Girault

4(2) Tarsi 4-segmented, the apical segment about twice as long as penultimate segment .... *Eofoersteria* Mathot
– Tarsi 5-segmented, with apical segment about as long as penultimate segment 5

5(4) Propodeum with translucent, mesh-like lamellae (Figs. 61–64, 66); forewing relatively broad, with numerous, scattered microtrichia (Fig. 114) ..... *Stephanocampta* Mathot
– Propodeum without such lamellae (Figs. 67–70, 72); forewing relatively narrow, with few microtrichia in one or two rows (Figs. 112, 113) ..... *Camptoptera*

Callodicopus Ogloblin
(Figs. 37–42, 73–78, 89, 90, 106, 115, 116, 125, 126)

Callodicopus Ogloblin 1955: 377; Yoshimoto 1990: 26. Type species: *C. crassula* Ogloblin, by original designation.
Decamymar Annecke 1961: 68. **Syn. nov.** Type species: *D. magniclavae* Annecke, by original designation.

Diagnosis. Body length ca. 0.36–0.9 mm. Occiput with a median vertical groove extending from foramen to vertex and either a distinct, angled, tranverse groove or sclerotized bar extending just above the foramen laterally to either a posterior extension of supraorbital trabcula or to a curved lateral groove originating from posterior apex of supraorbital trabecula (Fig. 41). Mandible 2-toothed (Fig. 42). Female funicle 7-segmented with F2 either ring-like (Fig. 126) or not (Fig. 125). Male flagellum 10-segmented with F2 ring-like. Forewing with posterior margin straight, the wing widening gradually towards apex (Figs. 114, 115, and Yoshimoto 1990, fig. 65). Proximal and distal macrochaeta present and moderately long (Figs. 115, 116). Procoxae widely separated by the broad anterior apex of prosternum. Prosternum anteriorly broad and truncate. Tarsi 5-segmented. Scutellum without transverse row of fovea. Mesophragma extending into gaster (Fig. 106). Propodeum only about one-quarter as long as scutellum (Fig. 78). Propodeal foramen broad, almost touching metacoxal foramen (Fig. 106). Petiole apparently absent.

Ogloblin (1955) described three other genera in addition to *Callodicopus* and suggested that all of them, together with *Dicopus*, could be considered to form their own tribe. *Dicopus* and Ogloblin's *Dicopomorpha* (with its synonyms *Dicopulus* and *Chromodicopus*) indeed appear to be fairly closely related and belong to the *Alaptus* group of genera. We exclude *Callodicopus* species because they have an occiput and scutellum similar to those of other *Camptoptera* group genera. We consider this to be more important in showing the true affinities of *Callodicopus* than the relatively broad attachment of the gaster to the propodeum, lack of distinct narrow petiole, and projection of the mesophragma into the gaster. Consequently, we place *Callodicopus* in the *Camptoptera* group.

We synonymize *Decamymar*, with one described species from Africa, under *Callodicopus* after examination of the two paratypes of *D. magniclavae* (SANC). Most of the described features are the same as for *Callodicopus*, but the transverse thickening above the occipital foramen that occurs in South American species is replaced by a line or groove.

Biology. Unknown.

Distribution. USA (Florida), Central and South America, southern Africa.

Key. Ogloblin (1955) for Argentina.

Included species. *C. crassula*, *C. longicornis* Ogloblin, *C. silvestrana* Ogloblin, *C. cursor* Ogloblin, *C. magniclavae*, **comb. n.**

Camptoptera Förster

(Figs. 31–36, 67–72, 87–88, 103–105, 112, 113, 123, 124)

Camptoptera Förster, 1856: 116, 119, 144; Girault 1909: 22; Annecke and Doutt 1961: 15; Soyka 1961: 73; Schauff 1984: 39; Noyes and Valentine 1989: 29; Yoshimoto 1990: 32. Type species: *C. papaveris* Förster, by monotypy.

Camptoptera (*Zemicamptoptera*) Ogloblin and Annecke, 1961: 24. Type species: *C.* (*Z.*) *semialbata* Ogloblin & Annecke, by original designation.

Congolia Ghesquière, 1942: 320. Type species: *C. sycophila* (Ghesquière), by original designation. Synonymy by Debauche (1949).

Eomymar Perkins, 1912: 26; Annecke and Doutt 1961: 16. **Syn. nov.** Type species: *E. muiri* Perkins, by monotypy.

Pteroclisis Förster, 1856: 144, unnecessary replacement name for *Camptoptera*. Two reasons why this name is unnecessary are that zoological and botanical names are independent of one another and there is at least a single letter difference in the names *Camptopteris* (a fossil plant) and *Camptoptera*.

Sphegilla Debauche, 1948: 62. Type species: *S. franciscae* Debauche, by original designation. Synonymy by Yoshimoto (1990).

Staneria Mathot, 1966: 214. **Syn. nov.** Type species: *S. diademata* Mathot, by original designation.

Stichothrix Förster, 1856: 117, 118, 121; Soyka 1953: 57. Type species: *S. cardui* Förster, by monotypy. Synonymy by Annecke and Doutt (1961).

Wertanekiella Soyka, 1961: 87. Type species: *W. brevicornis* Soyka. Synonymy under *Sphegilla* by Mathot (1969).

Diagnosis. Body length ca. 0.2–0.9 mm. Occiput with a median vertical groove extending from foramen to vertex and a distinct, curved, tranverse groove extending from eye to eye just above the foramen (Fig. 35). Mandible 1-toothed (Fig. 36). Female funicle 7-segmented, with F2 usually ring-like (Fig. 123) but sometimes only 6-segmented (species previously in *Sphegilla*, Fig. 124). Male flagellum 10-segmented with F2 and often F4 ring-like. Forewing with posterior margin almost always concave, giving the wing a distinctly curved apex (Figs. 112–113). Proximal macrochaeta absent and distal macrochaeta often relatively short and fine. Procoxae anteriorly abutting or slightly overlapping. Prosternum anteriorly narrow and pointed or curved. Tarsi 5-segmented. Scutellum without transverse row of fovea. Mesophragma not extending into gaster. Propodeum at least half as long as scutellum. Petiole as long as wide (Figs. 103–105), sometimes with a membranous collar encircling the petiole medially.

Eight genera and subgenera are treated here as synonyms of *Camptoptera*. We discuss them in more detail below, under three names in particular: a) *Sphegilla*, b) *Eomymar*, and c) *Staneria*.

a) Mathot (1969) synonymized *Wertanekiella* under *Sphegilla* which, in turn, was synonymized under *Camptoptera* by Yoshimoto (1990). Only females of the three described species of *Sphegilla* are known and they were stated to have six funicular segments and no ring segment (Debauche 1948; Taguchi 1971), though Yoshimoto (1990) stated that he had seen a definite annelliform F2 in the holotype of *S. franciscae* Debauche. We could not re-examine the type species of *Sphegilla* but a card-mounted specimen from Poland and two slide-mounted specimens of unidentified species

from Switzerland were seen. The Polish specimen differs from *S. franciscae* by the much longer scape and the Swiss specimens differ by the transverse instead of longitudingal striate sculpture on the mesoscutum, thus resembling *S. japonica* Taguchi. The Swiss specimens are very similar to *S. japonica* Taguchi and almost identical in thoracic sculpture to *Camptoptera* (*Zemicamptoptera*) *africana* Ogloblin & Annecke. All have a 6-segmented funicle with no trace of a ring segment (Fig. 124) and appear to be very similar to the two species of *C.* (*Zemicamptoptera*). Possibly, the elongate F2 may be the result of complete fusion of F2 with F3 but more likely F3 was simply lost entirely. A short but distinct gastral petiole is present in the Swiss specimens (the Polish specimens would require slide mounting to observe this feature). Debauche clearly was wrong in stating that a true abdominal petiole was absent. Species of *C.* (*Zemicamptoptera*) may well correspond to *Sphegilla* in that the reduction of male flagellomeres that Ogloblin and Annecke (1961) used to define their subgenus is paralleled by the loss of the ring segment, used in part to define females of *Sphegilla*.

It is illogical to maintain *Sphegilla* as a separate genus from *Camptoptera* on the basis of absence of a ring segment unless *Zemicamptoptera* is also given generic status. In both cases the species have all the features of a typical *Camptoptera* except for a reduction in the number of flagellomeres in males or funicular segments in females. Therefore, the synonymy of *Sphegilla* under *Camptoptera* proposed by Yoshimoto (1990) is upheld, the two described species of *Sphegilla* are transferred to *Camptoptera* as *C. franciscae* (Debauche), **comb. nov.**, and *C. japonica* (Taguchi) **comb. nov.**, and the single described species of *Wertanekiella* is transferred to *Camptoptera* as *C. brevicornis* (Soyka), **comb. nov.**

b) If we were to recognize *Zemicamptoptera* as a subgenus of *Camptoptera*, following Ogloblin and Annecke (1961), then *Eomymar* must also be treated as such and for essentially the same reason – an apparent change in number of funicular segments, but in females rather than males. We do not give *Eomymar* the status of a species group, let alone a subgenus, because there is really no change in number of flagellar segments in males or funicular segments in females with respect to most other *Camptoptera*. The only difference is that *C. muiri*, and *C. fenestratum* (Girault), both **comb. nov.** from *Eomymar*, have F2 in females similar in length to each of the remaining funicular segments instead of ring-like. A third species, *C. camptopteroides* (Girault), **comb. nov.** from *Eomymar*, has female F2 1.34 times as long as wide but only one-quarter the length of F3. It is thus intermediate between a ring segment as in most *Camptoptera* and a normal segment as in *C. muiri* and *C. fenestratum*. The ring segment can thus be considered as a derived feature that evolved as a progressive reduction in length of F2. The fourth species described in *Eomymar*, *E. maximus* Girault, is here transferred to *Mimalaptus* as *M. maximus* (Girault), **comb. nov.** The type slide of *C. muiri* bears four females and one male under a single coverslip. The intact female nearest the centre of the slide is here designated as lectotype in order to clarify application of the name *muiri* to the taxon.

Incidentally, Annecke and Doutt (1961) stated the ring segment was absent in males of *Eomymar*. Examination of the two species whose males are known (*C. camptopteroides* and *C. muiri*) confirm that the ring segment is indeed present. In addition, each of the following segments is constricted and slightly desclerotized just before the ring-like sclerotized apex. Thus, it appears that there are 7 more ring segments, one at the end of each flagellomere except the apical one.

c) Mathot (1966) stated that *Staneria* is close to *Camptoptera* but differs by the presence of placoid sensilla on the vertex, the position of the hypochaeta, and the form of the wings. His illustrations show a group of 4 placoid sensilla just medial to each lateral ocellus and the hypochaeta on the wing membrane behind the stigmal vein. The holotypes of *C. fenestratum* Girault and *C. camptopteroides* Girault (QMBA, examined) also have placoid sensilla and hypochaetae in the same relative positions, as do the illustrations of *C. scholli* Ogloblin and Annecke (1961). Only

the number of sensilla in each cluster varies, from 4 in *Staneria diademata* to about 14 in *C. camptopteroides*. The number of sensilla also varies from one side to the other of the same specimen, e.g., 6 and 9 in *E. fenestratum*. Ghesquière's (1942) illustration of the forewing base of *Congolia sycophila* Ghesquière resembles those of *Staneria diademata* Mathot and *C. scholli* in that all three species have a seta on the ventral surface of the disc behind the apex of the marginal vein or the stigma. Mathot (1966) called this seta the hypochaeta and used its position as one feature to separate *Staneria* from *Camptoptera*. If the position of this seta is of generic value then *Staneria* is a synonym of *Congolia*, on the basis of this feature at least, and so is *Eomymar*. But *Eomymar* is clearly a synonym of *Camptoptera* and we also concur with Debauche (1949) that *Congolia* is a synonym of *Camptoptera*. Thus, *Staneria* would remain generically distinct only on the presence of a group of placoid sensilla medial to each lateral ocellus. We cannot but agree with Ogloblin and Annecke that species with this feature belong in *Camptoptera*. Thus, we synonymize *Staneria* under *Camptoptera* and transfer its type species to *Camptoptera* as *C. diademata* **comb. nov.**

Biology. Species of ten families are reported as hosts for *Camptoptera* (including *Eomymar*): Coleoptera – Buprestidae; Homoptera – Aleyrodidae, Cicadellidae, Delphacidae, Kerriidae; Hymenoptera – Braconidae, Cynipidae; Lepidoptera – Tortricidae; Thysanoptera – Thripidae; and Coleoptera – Scolytidae, (Huber 1986, 1997). An additional, unpublished record (specimens received from K. Hoffman, Department of Entomology, Clemson University) is from *Derodontus* (Derodontidae). Most of the host associations require confirmation. The scolytid record is based on three specimens (CNCI) laboratory reared from eggs of *Pityophthorus tuberculatus* Eichhoff collected on *Pinus contorta* on 25.vii.1990, 20 km S. at Swan Hills, Alberta, Canada.

Distribution. Worldwide.

Keys. Regional keys to some of the described species are follows: Girault (1909) for North America; Ogloblin (1947) for Argentina; Soyka (1953, 1961) for Europe; Ogloblin and Annecke (1961) for Africa; Viggiani (1978b) and Subba Rao (1989) for India and Sri Lanka.

Included species. Seventy-four described species (Table I).

Discussion. *Camptoptera* is by far the most speciose genus of the *Camptoptera* group. Individuals are common and morphologically diverse, as mentioned already by Debauche (1948) and Noyes and Valentine (1989), especially in tropical forests. Because *Camptoptera* contains so many species it would be very useful if the genus could be divided into meaningful species groups. A thorough review of all characters across all species is necessary to determine how this should best be done. One could envisage two species groups, very unequal in number of species in each, that differ in the number of male flagellomeres or female funicular segments, analogous to the situation in *Anaphes* Huber (1992). The *armata* group, currently including most of the species, would be defined by having the normal complement of male and female antennal segments and the *semialbata* group would be defined by the reduction in the number of male flagellomeres from 10 to 7 or female funicular segments from 7 to 6. The latter group would correspond to Ogloblin and Annecke's (1961) *C.* (*Zemicamptoptera*) and Debauche's (1948) *Sphegilla*. Unfortunately, *Camptoptera* (*Z.*) *semialbata* and, according to Yoshimoto (1990), *Sphegilla franciscae* apparently have a ring segment so the groups are not completely distinct. We certainly do not consider it useful to treat either *C.* (*Zemicamptoptera*) or *Sphegilla* as subgenera. A better method would be to ignore number or relative lengths of antennal segments and define species groups on features such as propodeal structure, which shows considerable variety among the species. For example, many species have minute spicules on the median part of the propodeum and lack sublateral carinae whereas others seem to lack spicules but have strong parallel carinae on the propodeum, e.g., *C. matcheta* Subba Rao. This species, or perhaps a similar one from Borneo (UCDC, examined), also differs from typical *Camptoptera* in having an almost vertical, flat propodeum overhung dorsally

TABLE I. Checklist of *Camptoptera* species. The genus or subgenus in which each species was originally placed is given in parentheses when it differs from the nominate genus.

aequilonga Soyka, 1961: 85
africana Ogloblin & Annecke, 1961: 305 (subgenus *Zemicamptoptera*)
ambrae Viggiani, 1978b: 152
andradae Soyka, 1961: 75
angustipennis Ogloblin, 1947: 504
annulata Soyka, 1961: 76
aula Debauche, 1948: 71
brevicornis (Soyka), 1961: 88 (*Wertanekiella*)
brevifuniculata Subba Rao, 1989: 162
brunnea Dozier, 1933: 97
camptopteroides (Girault), 1916: 208 (*Eomymar*)
cardui (Förster), 1856: 121 (*Stichothrix*)
clavata Provancher, 1888: 404
cloacae Taguchi, 1972: 228
colorata Soyka, 1961: 77
concava Taguchi, 1972: 225
diademata Mathot, 1966: 216 (*Staneria*)
dravida Subba Rao, 1989: 163
dryophantae Kieffer, 1902: 8
ellifranzae zur Strassen, 1950: 145
elongatula Kryger, 1950: 46
fenestrarum (Girault), 1918: 198 (*Eomymar*)
foersteri Girault, 1917: 20
franciscae (Debauche) 1948: 63 (*Sphegilla*)
gregi Girault, 1913: 107
gschnitzi Soyka, 1961: 77
hundsheimensis Soyka, 1961: 78
immensa Girault, 1933: 5
intermedia Soyka, 1961: 75
interposita Soyka, 1961: 79
japonica (Taguchi), 1971: 52 (*Sphegilla*)
kannada Subba Rao 1989: 163
kressbachi Soyka, 1961: 80
lapponica Hedqvist, 1954: 275
longifuniculata Viggiani, 1978b: 153
loretoensis Ogloblin, 1947: 495
magna Soyka, 1946: 43
matcheta Subba Rao, 1989: 161
minorui Taguchi, 1971: 49
minutissima Dozier, 1932: 89
missionica Ogloblin, 1947: 499
muiri (Perkins 1912) (*Eomymar*)
nigra Soyka, 1961: 81
nigrosimilis Soyka, 1961: 81
okadomei Taguchi, 1972: 224

TABLE I – continued

papaveris Förster, 1856: 119
parva Soyka, 1961: 85
pechlaneri (Soyka), 1953: 58 (*Stichothrix*)
peripilosa Soyka, 1961: 83
perineti Risbec, 1952: 436 (*Stichothrix*)
philippina Taguchi, 1972: 223
pretoriensis Ogloblin & Annecke, 1961: 293
protuberculata Viggiani, 1978b: 155
psocivora Mathot, 1972: 392
pulla Girault, 1909: 27
reticulata Ogloblin, 1947: 501
saintpierrei Girault, 1915: 154 (probably an invalid name for *papaveris* Girault 1909 nec Förster)
sakaii Taguchi, 1977: 143
scholli Ogloblin & Annecke, 1961: 299
semialbata Ogloblin & Annecke, 1961: 302 (subgenus *Zemicamptoptera*)
serenellae Viggiani, 1978b: 151
setipaupera Soyka, 1961: 84
signatipennis Soyka, 1961: 85
stammeri (Soyka), 1953: 5 (*Stichothrix*)
strobilicola Hedqvist, 1956: 37
sycophila (Ghesquière), 1942: 321 (*Congolia*)
taenia Taguchi, 1972: 225
taiwana Taguchi, 1977: 144
tarsalis Kryger, 1950: 47
tenuis Soyka, 1961: 85
tuberculata Viggiani, 1978b: 154
vanharteni Viggiani & Jesu, 1995: 99
vinea Taguchi, 1972: 227
yamagishii Taguchi, 1971: 51

by the posterior apex of the scutellum, in contrast to an often more rounded and sloping propodeum that appears to merge evenly with the scutellum (Fig. 68). Study of body features such as these may yield a better understanding of the species diversity within *Camptoptera* and may even lead to the generic limits being modified again.

Camptopteroides Viggiani

(Figs. 1–18, 43–54, 79–82, 91–96, 107–109, 117–120)

Camptopteroides Viggiani 1974: 3. Type species: *C. armata* Viggiani, by original designation.
Paranagroidea Noyes and Valentine 1989: 44. **Syn. nov.** Type species: *P. verrucosa* Noyes and Valentine, by original designation.

Diagnosis. Body length ca. 0.6–1.13 mm. Occiput with or without a median vertical groove extending from foramen to vertex and an angled or curved transverse groove extending to or towards eye (Figs. 11, 17). Mandible 2-toothed (Figs. 12, 18). Female funicle usually 7-segmented with F2

ring-like, either slightly shorter (Fig. 4) or slightly longer than wide, but sometimes 6-segmented, with the ring segment absent (one species from Indonesia, Sulawesi, CNCI). Male flagellum 10-segmented with F2 ring-like (Fig. 5). Both sexes either macropterous or micropterous. Gaster sometimes compressed. Forewing in macropterous specimens straight, usually parallel-sided and apically pointed in females (Figs. 1, 107, 108) or uniformly broadening towards apex in males (Fig. 3) and some females, and usually maculate (Fig. 107–109), but often wings more or less reduced (Fig. 108), and the forewing disc with few (females) to several (males) microtrichia, especially at apex. Proximal and distal macrochaetae both present (Figs. 1, 3, 107–109). Procoxae widely separated by the broad anterior apex of prosternum. Prosternum anteriorly broad and truncate (Figs. 47, 53). Scutellum with transverse row of fovea. Tarsi 5-segmented. Mesophragma not extending into gaster. Propodeum about as long as scutellum (Figs. 43, 49, 54). Petiole as long as wide (Figs. 91–96).

Camptopteroides species are most easily recognized by the more or less distinctly patterned forewing, and heavy reticulation and long, thick setae on head and mesosoma. *Camptopteroides* is most similar to *Macrocamptoptera*. Both genera are relatively large and robust with the propodeum distinctly reticulate. The long, distinct macrochaetae of *Camptopteroides* distinguish them from *Macrocamptoptera*, which have short, inconspicuous macrochaetae. An undescribed male from Costa Rica (UCRC) has a wing shape more resembling *Macrocamptoptera* than *Camptopteroides*, though it has the long macrochaetae of the latter. The prosternum is hidden by the head and cannot be examined until the specimen is slide-mounted.

Males tend to be macropterous and in the New World at least no brachypterous males have yet been found. Brachypterous or micropterous females occur much more frequently in the Old World whereas only one micropterous female (Dominican Republic, CNCI) has been found so far in the New World.

Biology. Unknown.

Distribution. *C.* (*Camptopteroides*) – Australian (Australia, Fiji, New Zealand), Oriental (India, Indonesia, China, Vietnam), and Neotropical regions (Dominican Republic); *C.* (*Alalinda*) – Nearctic (USA) and Neotropical (Mexico, Central and South America) regions.

Included species. *C.* (*Camptopteroides*) *alata* Lin, **sp. nov.**, *C.* (*Camptopteroides*) *armata*, *C.* (*Camptopteroides*) *verrucosa*, **comb. nov.**, *C.* (*Alalinda*) *dorothea* Huber, **subgen**. and **sp. nov.**

Discussion. In their description of *Paranagroidea*, Noyes and Valentine (1989) did not count the anelliform segment of females as a segment, though they did for males and in their generic key. For consistency, it should be counted as one of the segments, when present.

Two subgenera are recognized, one of which is newly described below. Only one apparently constant character distinguishes each subgenus – the nature of the occipital suture. Other features help to distinguish the two but are not constant. These are discussed under *Camptopteroides* (*Alalinda*).

C. (*Alalinda*) was initially thought (by JH) to be a *Macrocamptoptera* or (by C. Yoshimoto) a *Callodicopus* but it is best placed within *Camptopteroides*. *C.* (*Alalinda*) would key to *Camptoptera* (including *Macrocamptoptera*) in Huber (1997) but differs by the patterned forewing with long macrochaetae, the median vertical occipital sulcus, and the parallel sides of the prosternum.

Macropterous females of *C.* (*Camptopteroides*), at least in the old world, have narrower, almost parallel-sided wings (Figs. 1, 107) compared to *C.* (*Alalinda*) (Fig. 109) whereas males of both subgenera usually have wings that widen distinctly and uniformly towards the apex (Fig. 3). *C.* (*Camptopteroides*) species tend to be more heavily sculptured, especially on the head, than *C.* (*Alalinda*) species. The presence of a median vertical suture above the occiput varies; most new world species have it and most old world species don't, but exceptions occur in each region.

C. (*Camptopteroides*) have a straight malar sulcus whereas *C.* (*Alalinda*) have a more or less strongly curved malar sulcus.

Several undescribed species are represented in various collections (ANIC, CNCI, QMBA, BMNH) but only *C. verrucosa* (Noyes and Valentine 1989), **comb. nov.** from *Paranagroidea*, from New Zealand and *C. armata* from Ceylon are described. Two others are described below.

Camptopteroides (*Alalinda*) Huber, new subgenus

(Figs. 13–18, 49–54, 81–82, 94–96, 109, 120)

Type species. *Alalinda dorothea* Huber, new species.

Etymology of subgenus. A combination of Spanish words, "ala" meaning wing, and "linda" meaning pretty, referring to the patterned wings of all members of the subgenus. Gender feminine.

Diagnosis. *Camptopteroides* (*Alalinda*) is distinguished from the nominate subgenus by the sutures of the occiput. In *C.* (*Camptopteroides*) the occipital suture extends from eye to eye, in the form of a very broad and shallow W (Fig. 11) whereas in *C.* (*Alalinda*) it forms a broad upside down V not much wider than the occipital foramen (Fig. 17).

Description. Female. Colour. Head and mesosoma dark brown to black, metasoma usually yellow basally and ventrally with varying amounts of brown towards apex dorsally. Scape, pedicel and legs usually yellowish, varying to light brown, often with darker tibiae; flagellum dark brown. Wings with dark patterns and a pale spot subapically.

Head. Head (Figs. 13–17) about 1.8 times wider and 1.6 times higher than long, and in dorsal view broadly hemisperical with slightly concave posterior surface (Fig. 13). Face in anterior view distinctly narrowing between eyes, bordered laterally by curved frontal suture that curves laterally below eye then inward ventrally to lateral margin of mouth (Figs. 15, 16), and face in lateral view flat above and below toruli but abruptly receding just above mouth opening (Fig. 14). Toruli a little less than their own diameter from transverse trabecula (Fig. 15). Eye well developed, in lateral view, extending posteriorly almost to occiput dorsally but far from occiput ventrally so gena appearing triangular posteroventral to eye (Fig. 14). Malar space about half eye length and without malar sulcus (Fig. 14). Vertex in lateral view smoothly and evenly curved to face (Fig. 14), in dorsal view sharply margined at occiput (Figs. 14, 17). Ocelli low triangle with following approximate proportions: POL = 2.1, OOL = 0.6, LOL = 1.1, with posterior ocelli almost touching occiput (Fig. 13). Occiput dorsally with a fine median groove extending from sharp dorsal margin to just above foramen where it joins two lateral arms extending ventrolateral towards lower apex of eye, the grooves forming a distinct upside down Y (Fig. 17). Maxilla slender, about 3 times as long as wide and 3 times as long as triangular labium (Fig. 17). Setation of head as follows, with the setae along dorsal margin of eye and between posterior ocelli the largest: 2 and 2 on occiput above foramen; 1 and 1 between posterior ocelli; 2 anterolateral to anterior ocellus; 4 in two groups of 2 along eye margin, the anterior 2 lateral to upper face and the posterior 2 lateral to posterior ocelli; about 5 and 5 on face below toruli (3 laterally and 2 submedially); 2 and 2 between toruli; and 2 and 2 on malar space lateral to mouth margin.

Antenna. Radicle distinct, about one-third as long as rest of scape. Funicle 7-segmented, with F2 minute, ring-like and somewhat triangular so funicle often bent at that point, the antenna thus appearing double geniculate. Clava 1-segmented.

Mouthparts. Labrum with 1 seta. Mandible with 2 teeth (Fig. 18).

Mesosoma. About 1.4 times as long as high and 1.2 times as long as wide; uniformly curved dorsally in lateral view and entirely covered with reticulate scupture (Figs. 49–54). Pronotum (Figs. 50, 53) short, entire, not visible in dorsal view, with straight posterior margin medially and narrow lateral panels. Propleura (Figs. 51–53) flat and fitting tightly against ventral margins of

pronotum and lateral margins of prosternum. Prosternum (Figs. 51, 52) narrowly rectangular anteriorly, widening posterioly just in front of coxae and apparently with a fine median longitudinal line at least posteriorly. Mesothoracic spiracle small, oval, at posterodorsal angle of pronotum. Mesoscutum relatively short and strongly curved in lateral view (Fig. 50). Notauli narrow, almost parallel. Scutellum slightly wider than long, with gently curved anterior and posterior margins and a transverse curved row of fovea in anterior third separating anterior from posterior scutellum (Figs. 49, 54). Axilla (Figs. 50, 54) small, transversely rectangular, divided into two sections by median longitudinal line, and only very slightly advanced into mesoscutum. Mesopleuron (Fig. 50) long and narrow, almost horizontal, longitudinally divided by a narrow groove anteriorly and a thicker line of fovea posteriorly, and ventrally merging smoothly with mesosternum. Metanotum apparently absent, visible only as very narrow line of different sculpture at anterior margin of propodeum (Figs. 49, 54). Propodeum almost as long as scutellum and in lateral view apparently smoothly merging with it (Figs. 50, 54). Propodeal spiracle minute; propodeal seta about halfway between spiracle and propodeal-metacoxal junction (Fig. 54). Setation of mesosoma as follows: pronotum with 1 and 1 setae submedially and 1 and 1 near posterolateral corners; mesoscutum with 1 and 1 strong sublateral setae in anterior half of midlobe and 1 and 1 near lateral angle of lateral lobe; axilla with 1 strong seta at anteromedian corner; scutellum with placoid sensilla widely separated, closer to axillar seta than to each other; propodeum with 1 and 1 propodeal seta about midway between posterior margin and spiracles.

Wings. Forewing (Fig. 109) narrow, widening uniformly towards apex, with posterior margin beyond venation almost straight and anterior margin towards apex strongly curved so apex distinctly asymmetrical. Colour pattern distinctive: membrane beyond venation with two dark areas separated by a clear area towards the apex. Marginal fringe with longest cilia distinctly longer than greatest wing width. Venation extending just over one-third wing length. Both macrochaetae and hypochaeta well developed and clearly visible, the distal macrochaeta about 3 times as long as proximal macrochaeta and the hypochaeta close to proximal macrochaeta.

Hindwing narrow and parallel-sided, with faint, uniform, brown suffusion broken by numerous, fine, clear transverse lines.

Legs. Coxa, especially hind coxae, distinctly reticulate. Tarsi 5-segmented, with first segment about 3 times as long as second. Foretibia with numerous short, thick spines. Foretibial spur bifurcate, with inner tine shorter than outer tine and their junction about halfway along spur length.

Metasoma. Gastral petiole (Figs. 94–96) narrow and distinct, slightly longer ventrally than dorsally, but shorter than wide or high. Gaster (Figs. 81, 82) with Gt_2 the longest tergum, Gt_3 slightly shorter, Gt_4–Gt_7 subequal in length and much shorter than Gt_7, Gt_8 laterally about twice as long as medially. Gt_8 with spiracle. Ovipositor arising in apical half of gaster and at most slightly exserted. Sterna broadly covered by terga; St_2 about as long as Gt_2, and anteriorly with reticulate sculpture; remaining sterna not clearly visible but probably equal in length to corresponding terga; St_6 (hypopygium) distinct, extending posteriorly to slightly beyond apex of gaster. Cercal plate with 3 long curved setae. Most terga with 1 and 1 long seta submedially and 1 and 1 shorter seta sublaterally, but Gt_3 with only 1 and 1 seta, Gt_8 with 2 and 2 lateral setae behind spiracle, and Gt_9 with 3 setae.

Male. Similar to female but metasoma usually entirely dark brown (except type species). Antenna with 10 flagellomeres, including a ring-like F2; radicle shorter than in female and not so distinct, about one-quarter total length of scape. Genitalia very similar to those of *C.* (*Camptopteroides*) (Viggiani 1989, and Fig. 6) but we consider that they are of his "type 2" rather than "type 3", in that aedeagal apodemes and digiti (with 3 teeth) are present and there is at least a partial sac-like encapsulation around the genitalia.

Distribution. Western Hemisphere, from USA (South Carolina, Missouri) south to Argentina. Several undescribed species occur in Central and South America. They differ in wing width, extend of brown maculation on the forewing and body sculpture. They are rarely collected and most are represented, in the CNCI at least, by only one or a few specimens, mainly females.

Camptopteroides (*Alalinda*) *dorothea* Huber, new species
(Fig. 109)

Type material. Holotype ♀ (CNCI), cleared and dissected, under 4 coverslips in Canada balsam on slide labelled as follows: 1. "*Camptopteroides* (*Alalinda*) *dorothea* Huber HOLOTYPE ♀ dorsal". 2. "SC: Anderson Co., Pendleton 25022m 17–27.vi,1987; FIT Mat. Hardwood Forest CNC Hym. Team".

PARATYPES. 6 ♀♀ and 1 ♂. USA: **Florida**: Alachua Co., Gainesville, AEI, iv–14.vii.1987, CNC Hym. Team (2 ♀♀ on points, CNC, USNM). **Missouri**: Wayne Co., Williamsville, 1–19.vi.1988, J.T. Becker (1 ♀ on point CNCI). **South Carolina**: Anderson Co., Pendleton, 250m, 13–18.v.1987, hardwood forest, CNC Hym. Team (1 ♀ on point); Dorchester Co. Francis Beidler forest, 10km NE Harleyville, 11–23.v.1987 and 26.v–11.vi; FIT, MT, bald cypress swamp (1 ♀ on point, 1 ♀ & 1 ♂ on slides, CNCI).

Biology. Hosts are unknown. Specimens were collected in Malaise or flight intercept traps in forests of various types.

Description. Female. Colour. Head and mesosoma dark brown, sometimes with faint green metallic reflections on head in certain lights. Radicle yellow, scape and pedicel yellowish except dorsal and ventral margins of scape and pedicel basally, brown. Funicular segments and clava dark brown. Coxae and trochanters dark brown (except sometimes middle coxa posteriorly or apically whitish), trochantelli whitish, femora of fore- and middle legs brown, sometimes with lighter areas, hind femur yellowish, tibiae and tarsi of all legs lighter brown than femora. Forewing (Fig. 109) with clear spot near apex poorly defined and merging indistinctly with surrounding brown areas.

Head. Head width (holotype) 296 µm. Vertex with isodiametric mesh-like sculpture except anteriorly along trabecula where sculpture is transverse.

Antenna. Measurements in m (n=2, holotype and one paratype). Mean (range in parentheses where needed) of length of each segment: radicle + scape 255 (252–258), pedicel 69 (65–72), F1 58, F2 15 (14–15), F3 69 (67–71), F4 55 (52–57), F6 53, F7 56, clava 275 (271–279). Length/width of funicular segments varies from 3.37 (F2) to 1.78 (F7). The clava has 4 longitudinal sensilla but the funicular segments lack these.

Mesosoma. Mesoscutum with fine, indistinct, somewhat transverse reticulate sculpture. Scutellum with indistinct, somewhat longitudinal scuplture medially, the sculpture becoming distinct laterally and on axilla. Metanotum medially and propodeum distinctly, deeply reticulate.

Metasoma. As described for genus.

Male. Colour as in female, but with a little more brown on gaster. Antennal measurements (n=1) as follows: radicle + scape 136, pedicel 55, F1–10 119, 7, 129, 132, 129, 121, 125, 122, 117, 116.

Etymology. The species is named in honour of my late mother, Dorothy Huber.

***Camptopteroides* (*Camptopteroides*) *alata* Lin, sp. nov.**
(Figs. 1 – 6)

Type material. Holotype ♀ (Fujian Agricultural University, Fuzhou, China) on slide, from Tongmu, Wuyishan Nature Reserve, Fujian, China, July 25, 1985, Lin Naiquan, collected by sweeping. Allotype ♂, with same collection data as holotype.

Diagnosis. The female of *C. alata* differs from *C. verrucosa* by an almost globular F4–F7 (F4–F7 distinctly longer than wide in *C. verrucosa*), a relatively longer ovipositor that is about 0.83X the length of the middle tibia (about 0.72X in *C. verrucosa*), and an eye that is longer than the malar space (shorter in *C. verrucosa*). The male of *C. alata* has a long, slender, pointed aedeagus (shorter, broader and bluntly rounded in *C. verrucosa*), more similar to the aedeagus of *C. armata*, which is somewhat intermediate between the two species. *C. armata* has only two spines on the digiti (Viggiani 1974, 1989), compared to three spines in *C. alata* and *C. verrucosa*. The female of *C. armata* is still unknown.

Description. Female. Body length 0.98 mm. Body dark brown to black; base of scape, F1, femora, tibiae, and tarsi pale yellow to testaceous; mandibles and wing venation, except for middle section of hind wing vein, dark brown. Eye dark reddish. Wings semihyaline, with yellow-brown suffusion, especially immediately behind venation and along wing margins.

Head (Fig. 3) in anterior view wider that long (78:60), with strong reticulate sculpture. Eye longer than malar space (30:22). POL about 15, equal to OOL.

Antenna (Fig. 4) with relative lengths of scape, pedicel, F1–F7, and clava as follows: 64:20:13:1:1.5:9:8:8:10:75. Scape about 4.3X as long as wide (64:15). F1 the longest funicular segment, almost twice as long as wide (13:7); F2 anelliform, about one-quarter as long as wide; F3–7 subequal in length, only F3 a little longer than wide (9:6.5); F4–F7 each about as long as wide. Each funicular segment, except F2, with flagellar setae arranged more or less in two whorls. Clava 2.6X as long as wide (75:29) and about 1.3X length of funicle (75:58), with 4 sensory ridges on dorsolateral surface.

Mesosoma longer than metasoma (110:85), with distinct reticulate sculpture, the reticulations almost the same size as on head. Axilla with long axillary seta almost at anteromedian angle. Propodeum about as long as mesoscutum (82:80).

Forewing (Fig. 1) about 8X as long as wide (178:22), parallel-sided, and with a few microtrichia on disc near apex and the longest fringe cilia (on anterior margin) about 4X as long as width of blade. Hind wing about 10X as long as wide (180:18), with a few microtrichia on disc near apex and the marginal cilia about 6X as long as blade width.

Fore- and hind leg with coxae distinctly reticulate and middle leg with coxa faintly reticulate. Proportions of femur:tibia:tarsi as follows: foreleg 58:49:62, middle leg 63:76:54, hind leg 75:80:63.

Metasoma shorter than mesosoma (85:110), without distinct sculpture. Gaster laterally compressed, with second tergum covering almost nine-tenths of gaster. Ovipositor about three-quarters length of metasoma (63:85) and four-fifths length of middle tibia (63:76), not exserted beyond gastral apex.

Male. Similar to female except as follows. Body length 1.14 mm. Antenna (Fig. 5) about 1.5X as long as body (463:250), with relative lengths of scape, pedicel, and F1–10 as follows: 43:14:44:2:46:46:47:44:45:44:44:43. Each flagellar segment except F2 more than 6X as long as wide and with 4 sensory ridges. F2 ring-like, wider than long. Fore- and hind wings (Fig. 2) increasing in width towards apex, with many more microtrichia on disc than in female. Genital capsule (Fig. 6) 0.22X as long as middle tibia (39:178). Aedeagal apodemes curved ventrally and 0.18X as long as middle tibia. Digiti each with three teeth.

Etymology. The specific epithet, *alata*, refers to the fully winged male of the species (as in *C. armata* but in contrast to *C. verrucosa*).

Eofoersteria Mathot
(Figs. 111, 127)

Eofoersteria Mathot 1966: 231. Type species, *E. camptopteroides* Mathot, by original designation.

Diagnosis. Body length ca. 0.25–0.32 mm. Occiput with a median vertical groove extending from foramen to vertex and curved transverse groove extending to lateral margin of head below eye. Mandible 1-toothed, sharply pointed. Female funicle 6-segmented, without a ring-like segment (Fig. 127). Procoxae anteriorly abutting. Prosternum anteriorly pointed. Scutellum without transverse row of fovea. Forewing slightly but distinctly curved (Fig. 111). Proximal macrochaetae absent, distal macrochaeta short. Tarsi 4-segmented. Propodeum at least half as long as scutellum. Petiole as long as wide.

The two main features that distinguish *Eofoersteria* from the other genera in the group are either a loss (funicle 6-segmented) or a fusion (4-segmented tarsi). On this basis *Eofoesteria* can be treated as a derived offshoot of *Camptoptera*.

Biology. Unknown.

Distribution. Afrotropical (Congo), Oriental (Ceylon), Australian (Australia), Nearctic (southern Florida), and Neotropical regions (Trinidad).

Key. Viggiani (1978a).

Included species. *E. camptopteroides*, *E. secunda* Viggiani, *E. vasta* (Girault), **comb. nov.** from *Camptoptera*.

Discussion. *Eofoersteria vasta* (Girault) is the third species to be added to the genus. Although Girault (1920) did not specify how many specimens he examined when describing this species it is certain that there is only one, so we follow Dahms (1986) in treating the only known specimen as the holotype. This specimen is on a slide with eight other specimens (under three coverslips) representing four other species of Hymenoptera. Dahms (1984: 662 and 1986: 628) confused the various species in his description of the position of the specimens on the type slide. Their positions are clarified as follows. The holotype female of *E. vasta* is the uppermost specimen on the coverslip partially filled with Canada balsam and nearest Girault's label. It is mounted ventral side up. The specimen immediately below this is a female *C. gregi* Girault. It is mounted dorsal side up and, as pointed out by Dahms (1984), it may or may not be one of the nine specimens of this species mentioned by Girault (1915). The remaining four specimens (3 ♀♀ and 1 ♂) under the same coverslip represent an unidentified *Alaptus* species. The middle coverslip fragment contains the holotype female of *Erythmelus pauciciliatus* Girault. The coverslip fragment furthest from Girault's label contains two unidentified Trichogrammatidae.

We report here a fourth species of *Eofoersteria* based on four females from Trinidad and southern Florida, thus extending the range of this genus into the New World. This species is not formally described at this time because of lack of sufficient material for proper study. It is the smallest species of the genus, measuring about 250 μm.

Because there are at least two reductions involving different parts of the body we maintain *Eofoersteria* as a distinct genus. Had there been only one reduction, e.g., in the number of funicular segments, we would probably have synonymized the genus under *Camptoptera* and treated it at most as a species group.

Mathot (1966) pointed out that the 4-segmented tarsi of *Eofoersteria* casts doubt on the subdivision of Mymaridae into subfamilies and tribes on the basis of tarsomere number. He also

stated that it wasn't much more satisfactory to base higher classification of Mymaridae on abdominal characters, as proposed by Annecke and Doutt (1961). While we agree with Mathot's first statement, we are not sure about his second, though evidence in the *Camptoptera* group suggests that the picture is more complex that previous classifications would suggest. The nature of the junction between mesosoma and metasoma is more complex than simply apparent loss or fusion of the petiole. The problem with this character complex is that there are intergrades, as shown by *Callodicopus*.

Reduction in tarsomere number from 5 to 4 has likely occurred several times in Mymaridae. In *Eofoersteria*, the apical tarsomere is at least twice as long as each of the remaining tarsomeres. Its length and the fact that it has about twice the number of setae as any of the previous segments means that it is a fusion of segments 4 and 5. The 6-segmented female funicle with no trace of a ring segment represents a complete loss of F2, similar to that found in at least one *Camptopteroides* (Fig. 119). Clearly, loss or perhaps fusion of segments, whether antennal or tarsal, occurs much more frequently than previously realized, necessitating a re-evaluation of generic limits in several groups. Unfortunately, in the past, too much reliance was placed on the number and constancy of appendage segments for defining genera, with the result that several genera, not only in the *Camptoptera* group, are too narrowly defined.

Macrocamptoptera Girault, revised status

(Figs. 19–24, 55–60, 83, 84, 97–99, 110, 121)

Macrocamptoptera Girault, 1910: 239. Type species: *Camptoptera metotarsa* Girault (1905), by original designation.
Herulia Hedqvist, 1962: 103. **Syn. nov.** Type species: *H. sundholmi* Hedqvist, by original designation.
Rhila Donev, 1989: 79. **Syn. nov.** Type species: *R. bulgarica* Donev, by original designation.
Camptoptera (*Macrocamptoptera*); Yoshimoto 1990: 34.

Diagnosis. Body length ca. 0.9–1.5 mm. Occiput with a median vertical groove extending from foramen to vertex but without a transverse groove extending to posterior extension of supraorbital trabecula (Fig. 23). Mandible 2-toothed (Fig. 24). Female funicle 7-segmented (Fig. 121). Male flagellum 10-segmented with F2 ring-like. Forewing relatively broad, and widening distinctly towards apex (Fig. 110). Proximal and distal macrochaetae present but short and indistinct (Fig. 110). Prosternum anteriorly broad and truncate (Fig. 57–59). Procoxae widely separated by the broad anterior apex of prosternum. Scutellum with transverse row of fovea (Fig. 55). Propodeum about as long as scutellum (Figs. 55, 60). Tarsi 5-segmented. Petiole longer than wide (Figs. 97–99).

Macrocamptoptera differs from *Camptopteroides*, the genus to which it is probably most closely related, by the relatively short and inconspicuous macrochetae and slightly incurved posterior margin of the forewing, the lack of a transverse groove on the occiput above the foramen (Fig. 23), and the shape of the prosternum (Fig. 57). Otherwise, its species are similar in general appearance to species of *Camptopteroides* (*Alalinda*).

Biology. Unknown. Although not common, *Macrocamptoptera* is fairly widespread and has mostly been collected in deciduous forests. In North America one series has been collected from yellow pan traps set on or around wood piles. The species may parasitize eggs of insects boring in wood.

Distribution. North America, Europe.

Included species. *M. metotarsa*, *M. sundholmi*, **comb. nov.** from *Herulia*, *M. bulgarica*, **comb. nov.** from *Herulia*.

Macrocamptoptera metotarsa occurs throughout eastern North America (CANADA: Ontario, Quebec. USA: Arkansas, Georgia, North Carolina, South Carolina, Florida, Tennessee) and as far west as Alberta, New Mexico and California (all specimens in CNCI). The forewing color pattern of *M. metotarsa* varies in the amount of infuscation (compare fig. 64 in Yoshimoto 1990 with Fig. 110 here). This may be due either to regional variation or simply whether specimens are fresh or faded. *Macrocamptoptera sundholmi* (Hedqvist) occurs in Sweden and Belgium (two specimens in CNCI) and *M. bulgarica* (Donev) is known only from the holotype from Bulgaria. The latter name may eventually prove to be a synonym of *M. sundholmi*. Soyka (1961) described *M. grangeri* from a single female from France. Viggiani and Jesu (1988) included it in *Camptoptera* but until we can examine the holotype we are uncertain whether it is a very small *Macrocamptoptera* or a large *Camptoptera*. It is not included in the list of *Camptoptera* species.

Discussion. Peck (1951) placed *Macrocamptoptera* under *Camptoptera* and this synonymy was accepted by Annecke and Doutt (1961) and Schauff (1984). Soyka (1961) and Noyes and Valentine (1989: 45) treated *Macrocamptoptera* as separate from *Camptoptera*. Yoshimoto (1990) treated it as a subgenus under *Camptoptera*. We re-affirm *Macrocamptoptera* as a genus separate from *Camptoptera*.

Taguchi (1971) synonymized *Herulia* without explanation under *Sphegilla*. Later, after examination of the holotype of *H. sundholmi*, Schauff (1984) synonymized *Herulia* under *Camptoptera*. He was correct in his placement only if one treats *Macrocamptoptera* as a synonym of *Camptoptera*. We synonymize *Herulia* under *Macrocamptoptera*; its type species, *M. sundholmi*, is very similar to *M. metotarsa* (Girault) in size and structure. We examined the holotype of *Rhila* (UPPH) and transfer it to *Macrocamptoptera* as *M. bulgarica* (Donev). The close relationship of *Macrocamptoptera* to *Camptopteroides* is re-enforced by the peculiar male from Costa Rica mentioned under *Camptopteroides* that has a wing shape resembling *Macrocamptoptera* but the long macrochaetae of *Camptopteroides*.

Stephanocampta Mathot

(Figs. 25–30, 61–66, 85, 86, 100–102, 114, 122)

Stephanocampta Mathot 1966: 219. Type species. *S. yaosekoensis* Mathot, by original designation. *Hadromymar* Yoshimoto 1990: **Syn. nov.** Type species. *H. masoni* Yoshimoto, by original designation.

Diagnosis. Body length ca. 0.35–0.65 mm. Occiput without a median vertical groove extending from foramen to vertex but with a curved transverse groove extending to lateral margin of head at about mid-eye height (Fig. 29). Mandible apparently 1-toothed (Fig. 30). Female funicle 7-segmented with F2 either subequal to remaining segments or ring-like; male flagellum 10-segmented with F1 about half as long as F3, and F2 and apparently F4 ring-like (only one male, in CNCI, from Costa Rica was seen). Procoxae anteriorly almost abutting (Figs. 63–65). Prosternum anteriorly pointed (Figs. 63–65). Scutellum without transverse row of fovea (Fig. 61). Forewing relatively broad, especially towards apex, and slightly curved, with numerous setae on disc (Fig. 114). Proximal macrochaeta present but distinctly shorter than distal macrochaeta (Fig. 114). Tarsi 5-segmented. Propodeum at least half as long as scutellum, with a set of rigid translucent membranous lamellae (Figs. 61–64, 66) somewhat resembling those found in *Ptilomymar* Annecke and Doutt. Petiole short, surrounded ventrally and laterally by translucent lacey collar extending out from base of gaster (Figs. 85, 86, 100–102).

Biology. Unknown.

Distribution. Afrotropical (Congo, Madagascar, Rwanda, Tanzania), Oriental (Indonesia, Malaysia), Nearctic (USA – Florida) and Neotropical regions (Costa Rica south to Brazil).

Included species. *S. yaosekoensis*, *S. masoni*, **comb. nov.** from *Hadromymar*.

Specimens of a species from Gabon (CNCI) have a relatively narrow translucent membrane on the propodeum somewhat as in *Stephanocampta*, but have narrow wings and a short F2 not quite as narrow as in most *Camptoptera*. They do not fit well in *Stephanocampta* and may represent just an aberrant *Camptoptera*. However, we prefer not assign them to a genus here, pending further study of the generic limits of *Camptoptera*.

Discussion. We synonymize *Hadromymar* under *Stephanocampta* because both nominal genera have the same, characteristic propodeal and gastral lamellae and relatively broad forewings. *Stephanocampta* is yet another genus of the group in which F2 of females may be normal or ringlike.

Conclusions

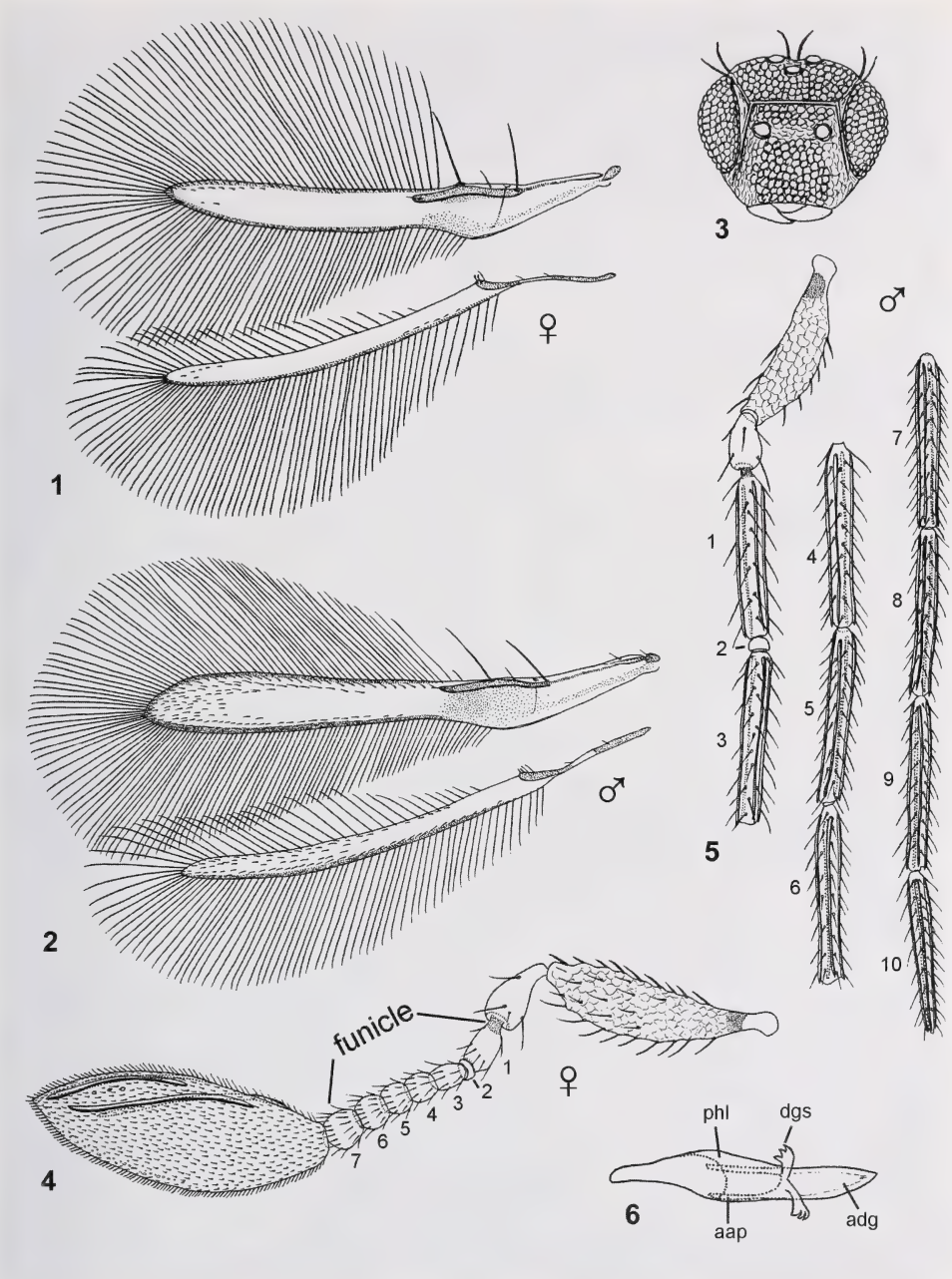
The results of this study illustrates weaknesses in the classification of mymarids as presented by previous workers.

First, the reduction of tarsomeres in Mymaridae from five to four has occurred in different ways and is not a unique occurrence. In *Eofoersteria* the reduction is a result of fusion of the apical two segments and not an outright loss as is apparently the case in other, unrelated genera with four tarsomeres. At least one subfamily classification (Debauche 1948) was based on the supposition that this change occured only once. At the generic level, change in the number of funicular segments of females or flagellar segments of males is also insufficient grounds for defining or proposing new genera unless well supported by changes in other characters. For example, at least three of the *Camptoptera*-group genera, *Camptoptera*, *Camptopteroides*, and *Stephanocampta*, have either 6 or 7 funicular segments in females. When 7 are present the relative length of F2 may vary from ringlike to normal as in *Camptoptera*, *Stephanocampta*, and *Callodicopus*.

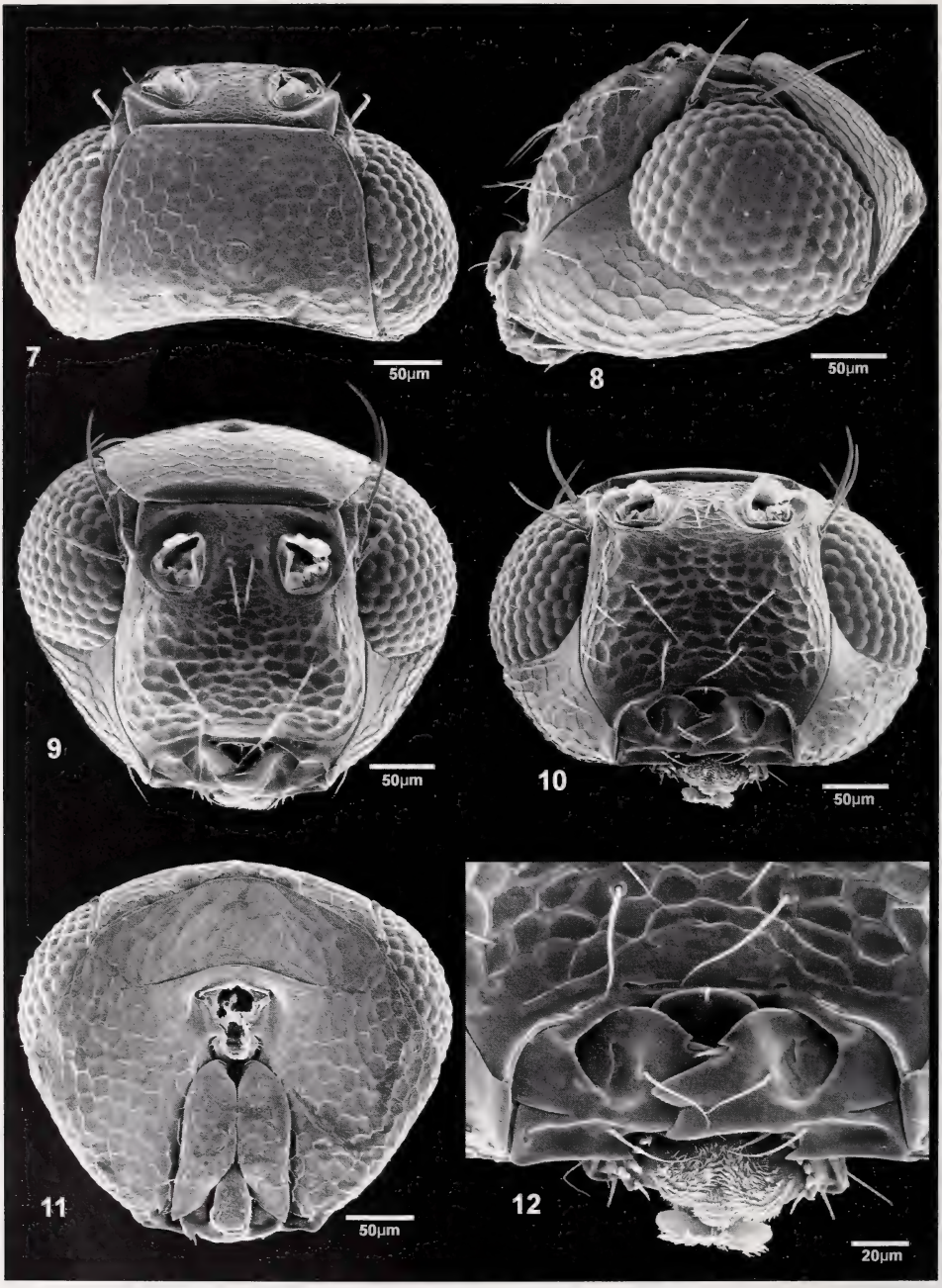
Second, the nature of the gastral petiole was portrayed in an overly simplistic manner in previous classifications. There appears to be more of a gradation in petiole length/width and the nature of attachment to the propodeum than was previously thought. Thus, in the *Camptoptera* group of genera the possibilities range from no visible petiole, with a relatively broad attachment of gaster to the propodeum (*Callodicopus*), to a petiole that is very narrow, slightly longer than wide, clearly distinct from the rest of the gaster, and with a relatively narrow attachment to the propodeum (as in *Camptoptera*).

Third, a given genus of Mymaridae is rarely restricted to only one major geographic region. Much more often a genus is found to occur in at least two and often most regions, a fact not fully appreciated by previous workers. Thus, to avoid creating inadvertent synonyms, new genera should be described only after studying a diversity of species from all related genera, regardless of their provenance. The relatively numerous synonymies proposed here are a result of examining material from all major zoogeographic regions.

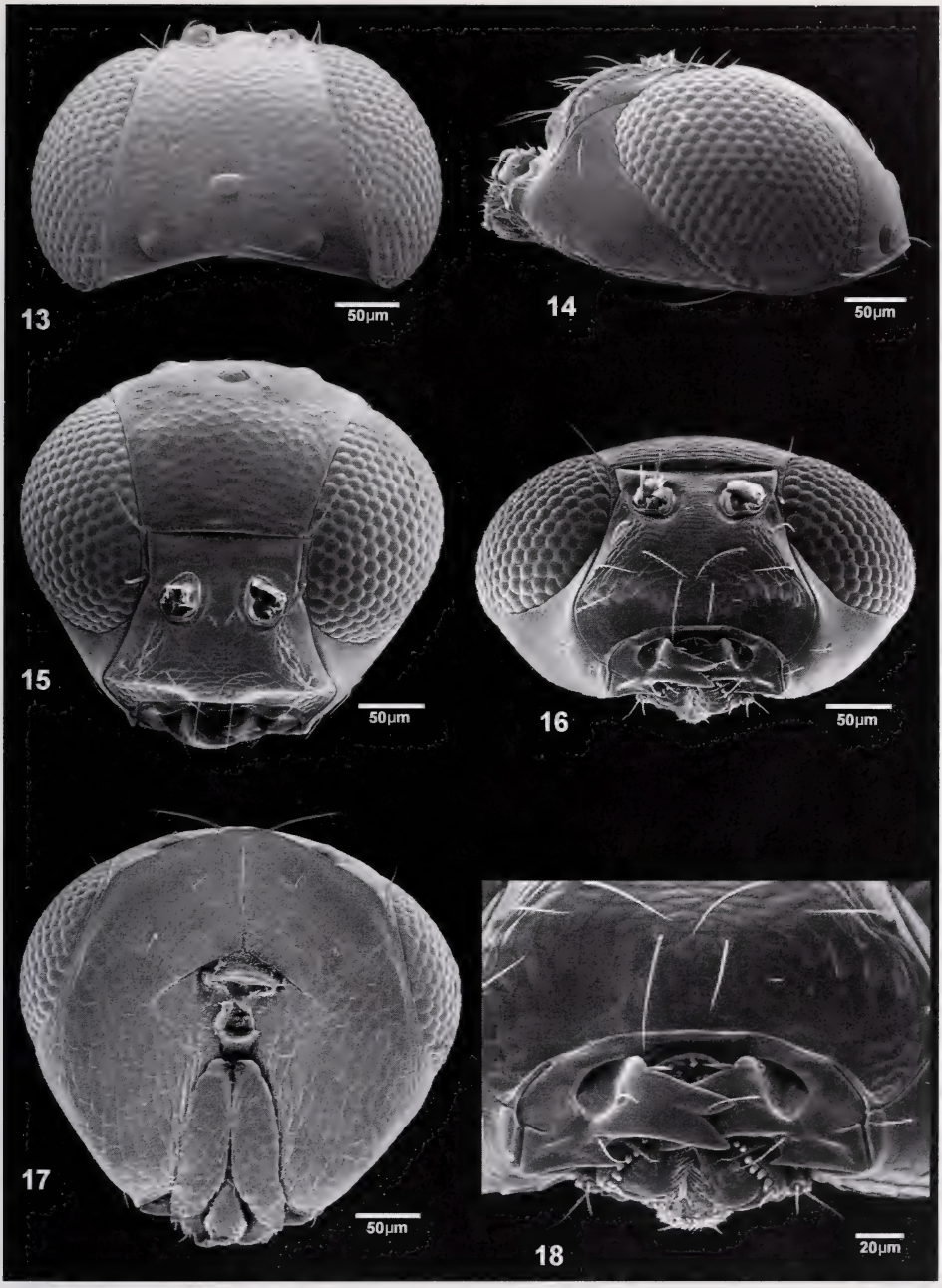
Finally, because most species within the *Camptoptera*-group of genera are small to minute many more new species will likely be found. Their discovery will undoubtedly lead to a better definition of *Camptoptera* at least, and perhaps proposal of yet more genera within the group. Until a more thorough knowledge of the diversity of *Camptoptera* species is obtained, based on study of greater numbers of good slide-mounted specimens, its generic limits, at least, will remain unclear. Similarly, the generic limits of the remaining genera may again have to be modified.



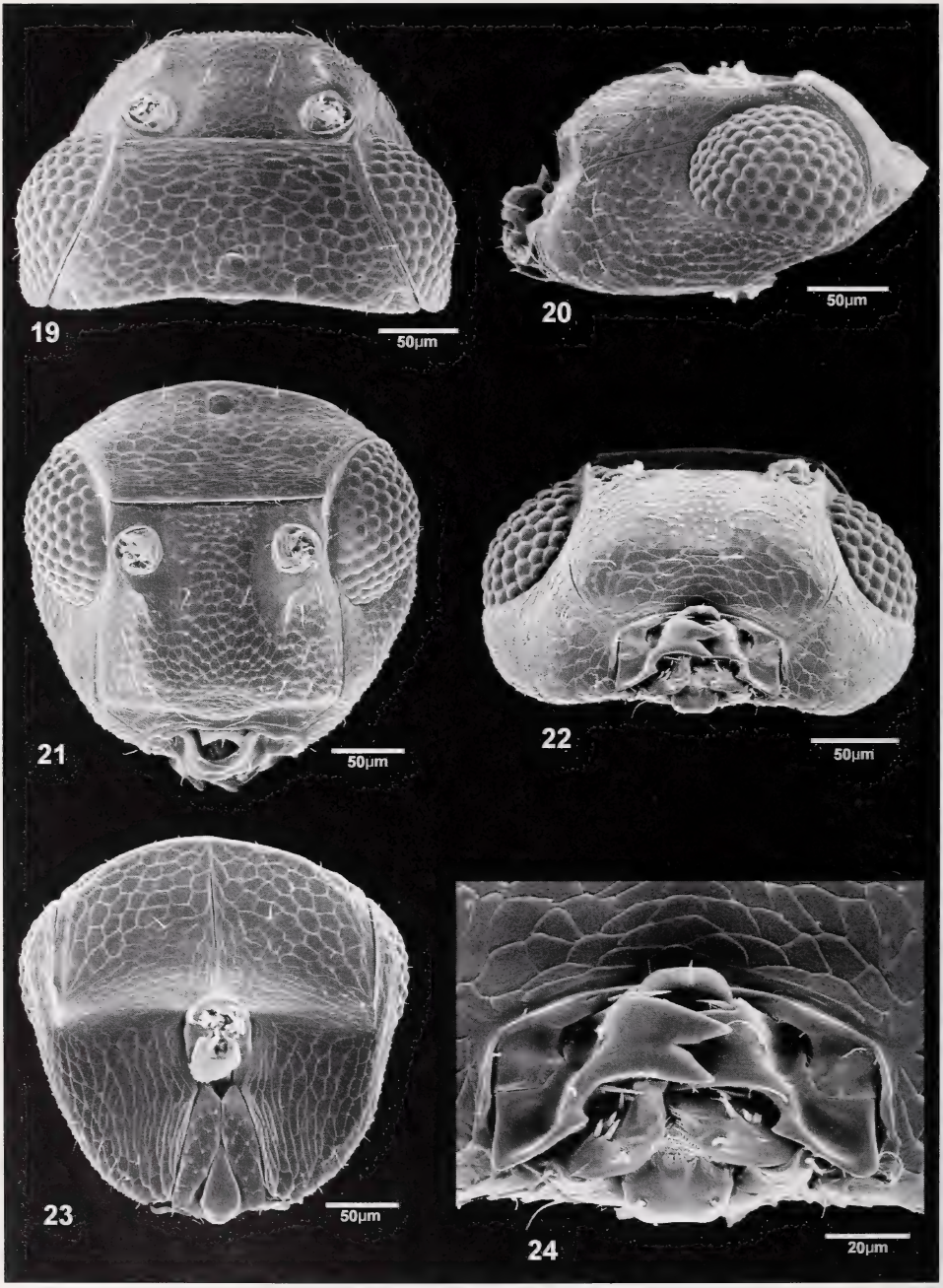
FIGURES 1–6. *Camptopteroides* (*Camptopteroides*) *alata* Lin. 1, ♀ wings; 2, ♂ wings; 3, head; 4, ♀ antenna; 5, ♂ antenna; 6, ♀ genitalia. Abbreviations: adg = aedeagus, dgs = digital spines, phl = phallobase.



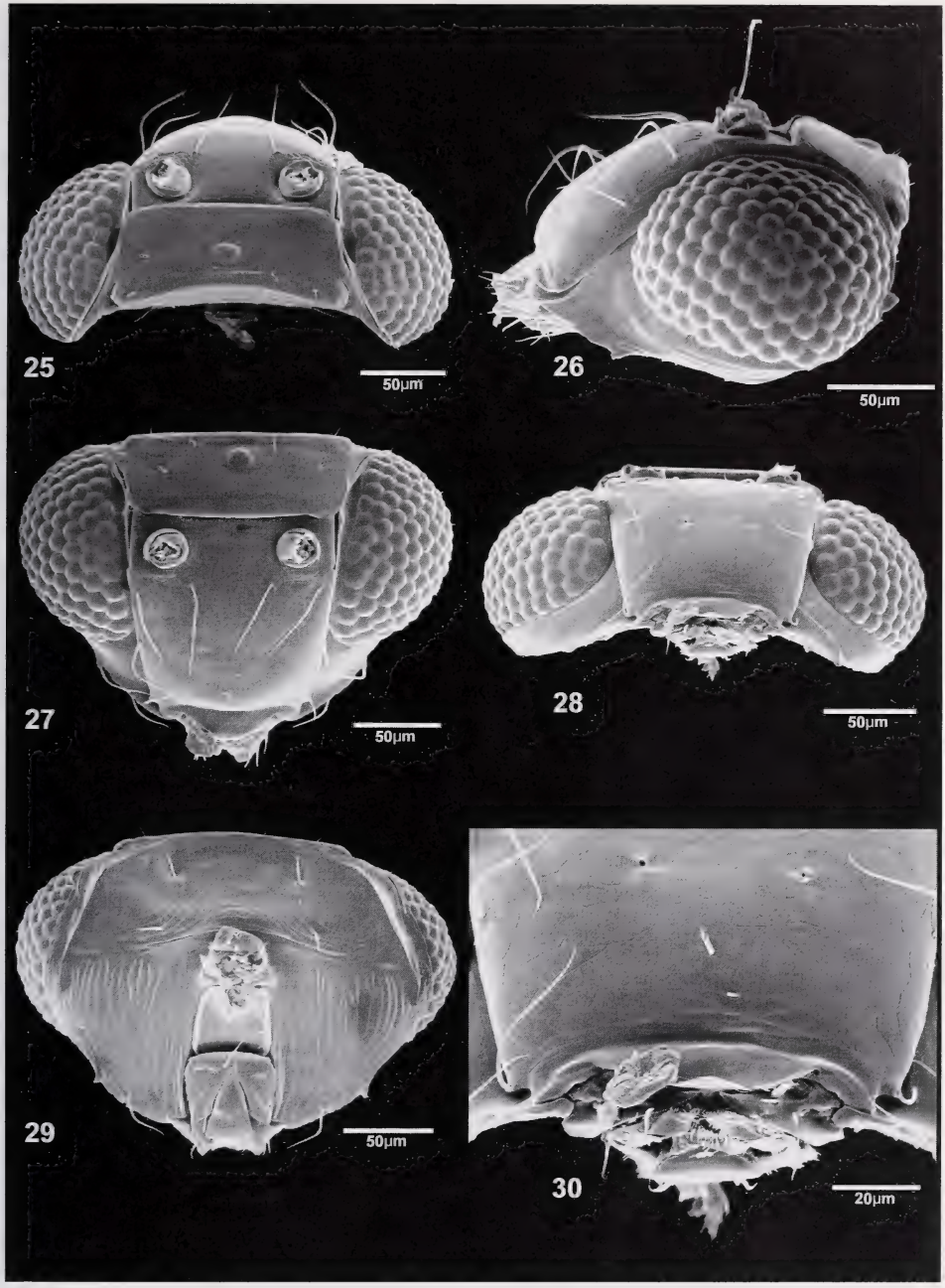
FIGURES 7–12. *Camptopteroides* (*Camptopteroides*) sp., Australia, Queensland, Mt. Lewis. 7–11, head: 7, dorsal; 8, lateral; 9, anterior; 10, ventral; 11, posterior; 12, mouthparts.



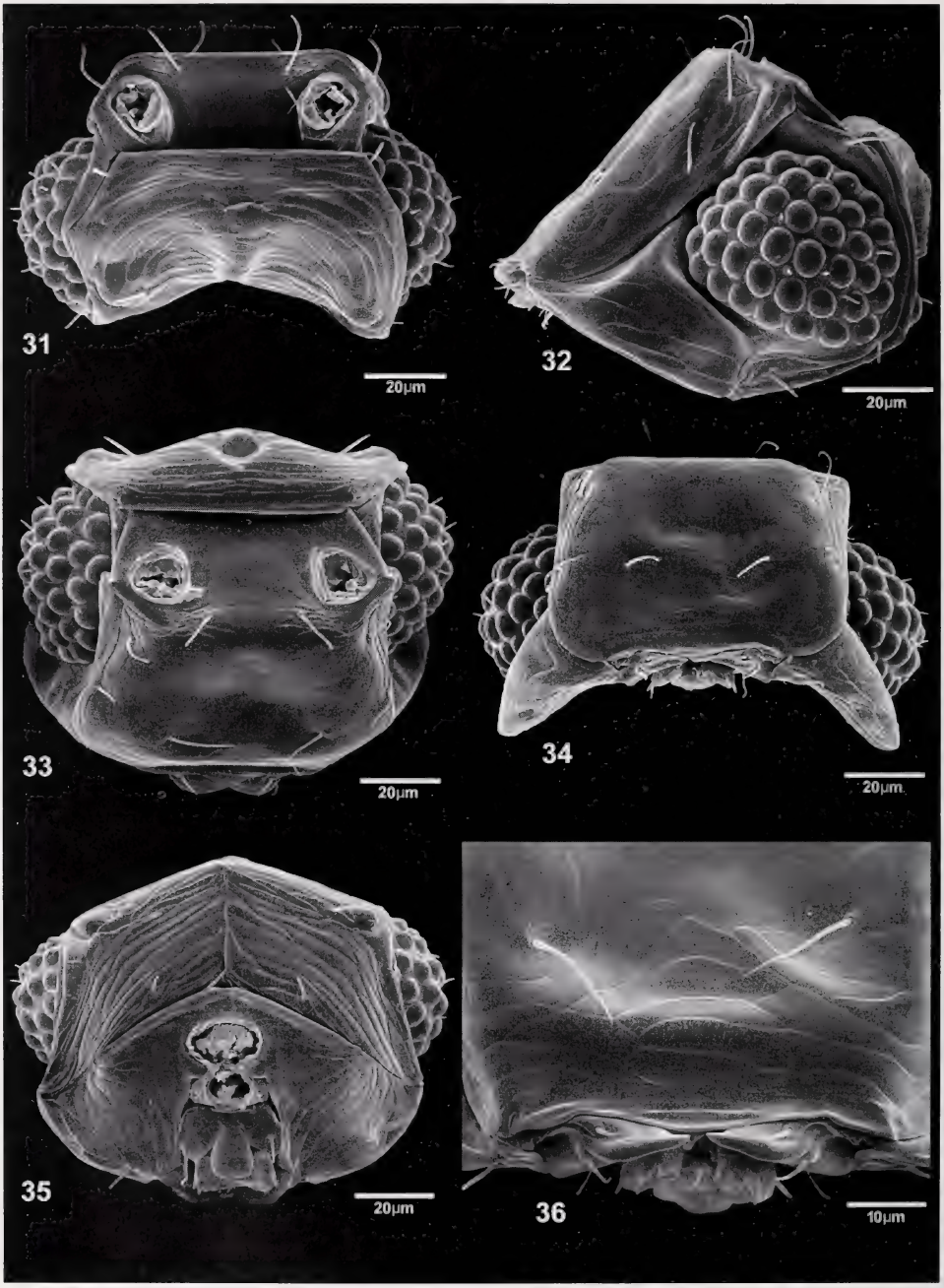
FIGURES 13–18. *Camptopteroides* (*Alalinda*) spp., Costa Rica, Limón, and Ecuador, Sucumbios, Sacha Lodge. 13–17, head: 13, dorsal; 14, lateral; 15, anterior, 16, ventral; 17, posterior; 18, mouthparts.



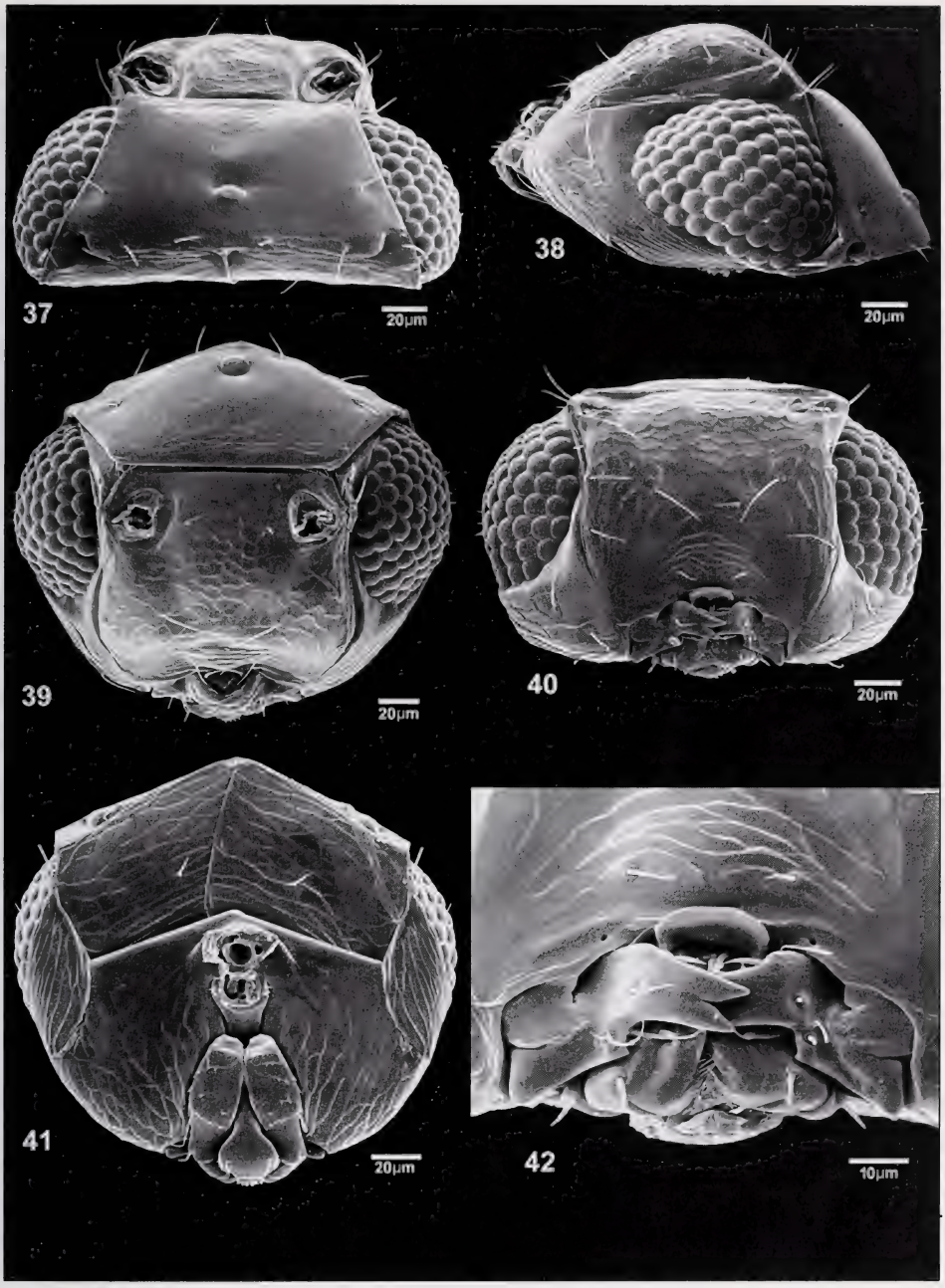
FIGURES 19–24. *Macrocamptoptera metotarsa* (Girault), USA, SC, Pendleton. 19–23, head: 19, dorsal; 20, lateral; 21, anterior, 22, ventral; 23, posterior; 24, mouthparts.



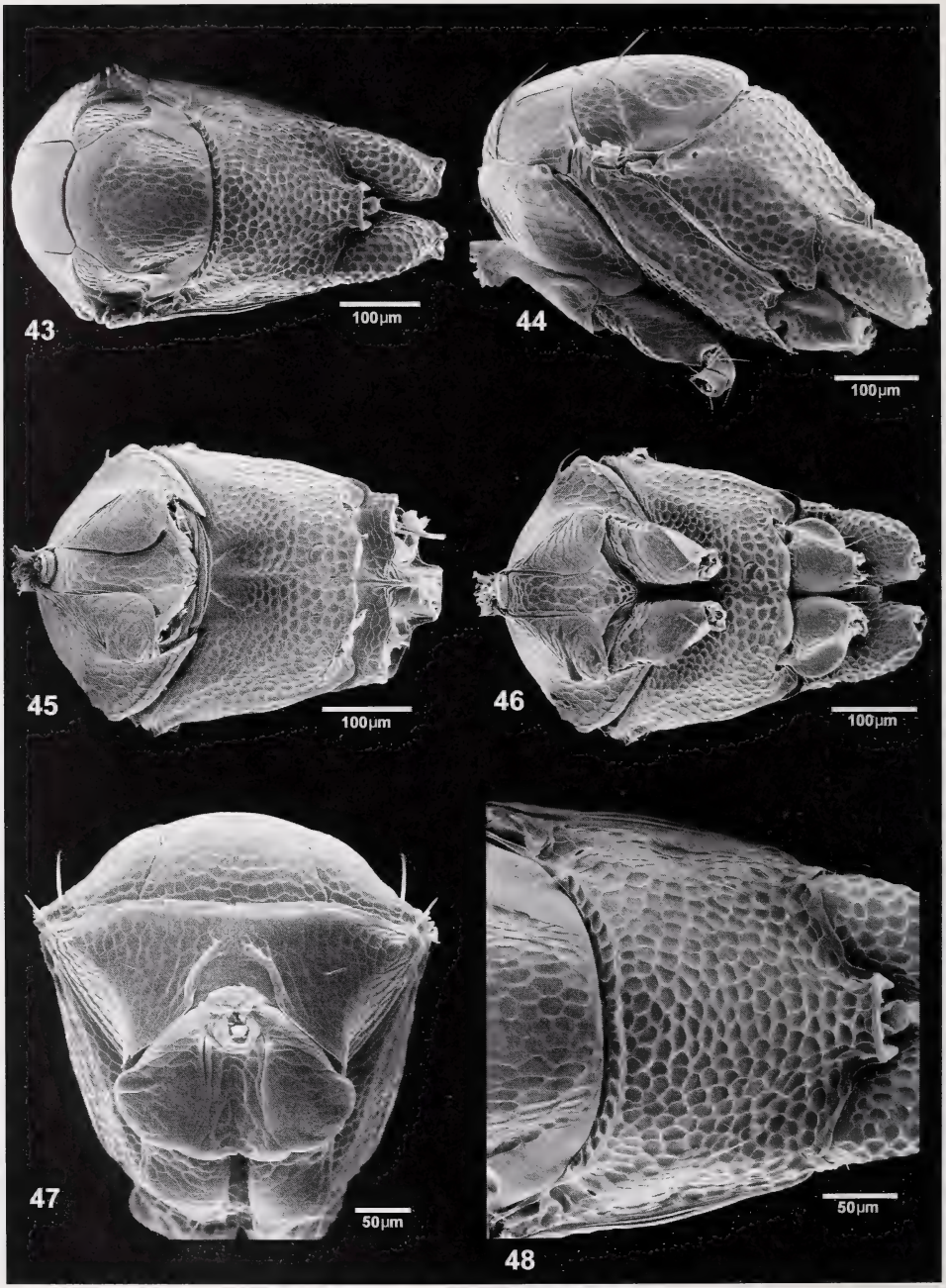
FIGURES 25–30. *Stephanocampta* sp., Ecuador, Napo, Sierra Azul. 25–29, head: 25, dorsal; 26, lateral; 27, anterior; 28, ventral; 29, posterior; 30, mouthparts.



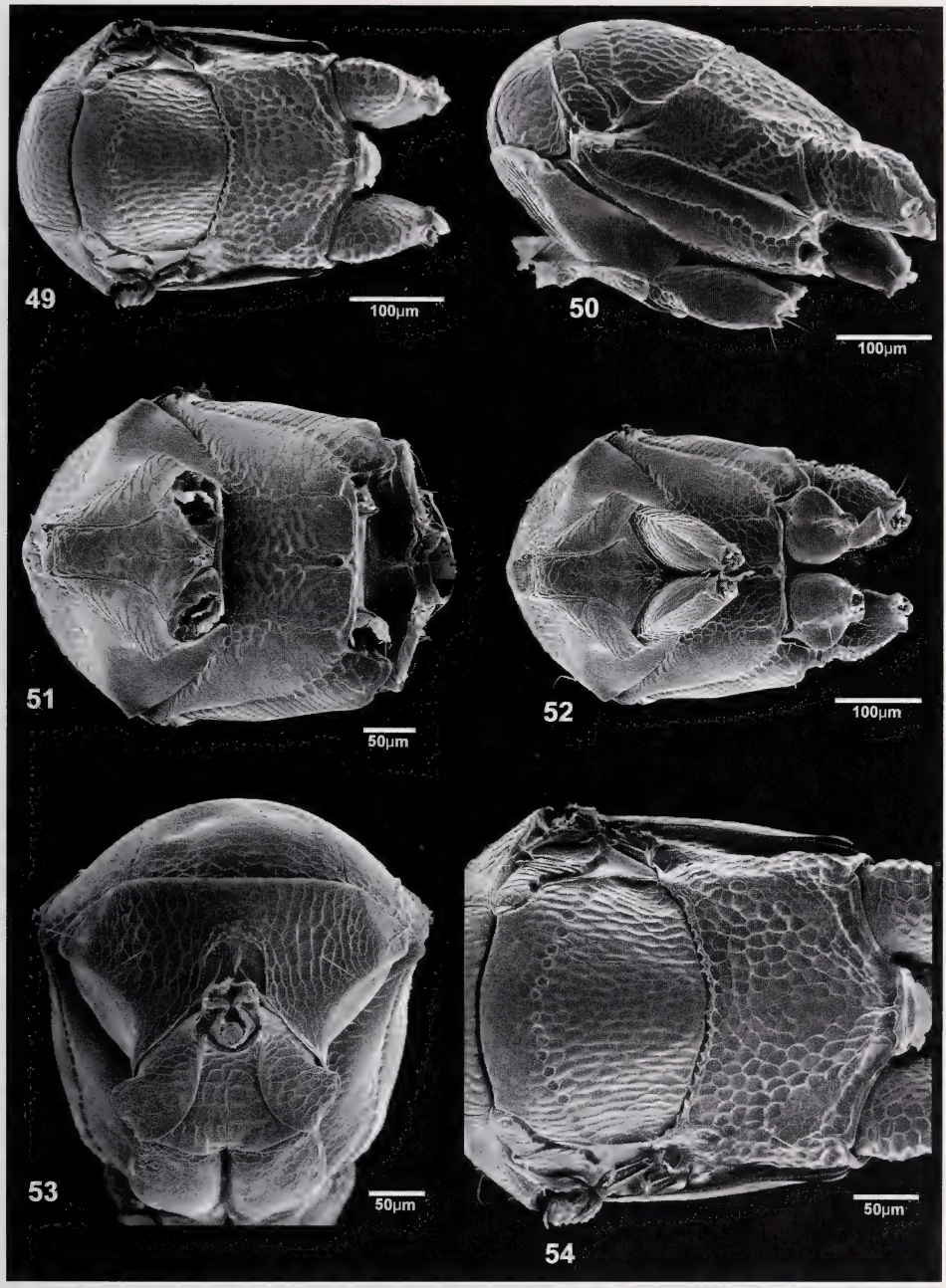
FIGURES 31–36. *Camptoptera* sp. USA, FL, Monroe Co., No Name Key. 31–35, head: 31, dorsal; 32, lateral; 33, anterior; 34, ventral; 35, posterior; 36, mouthparts.



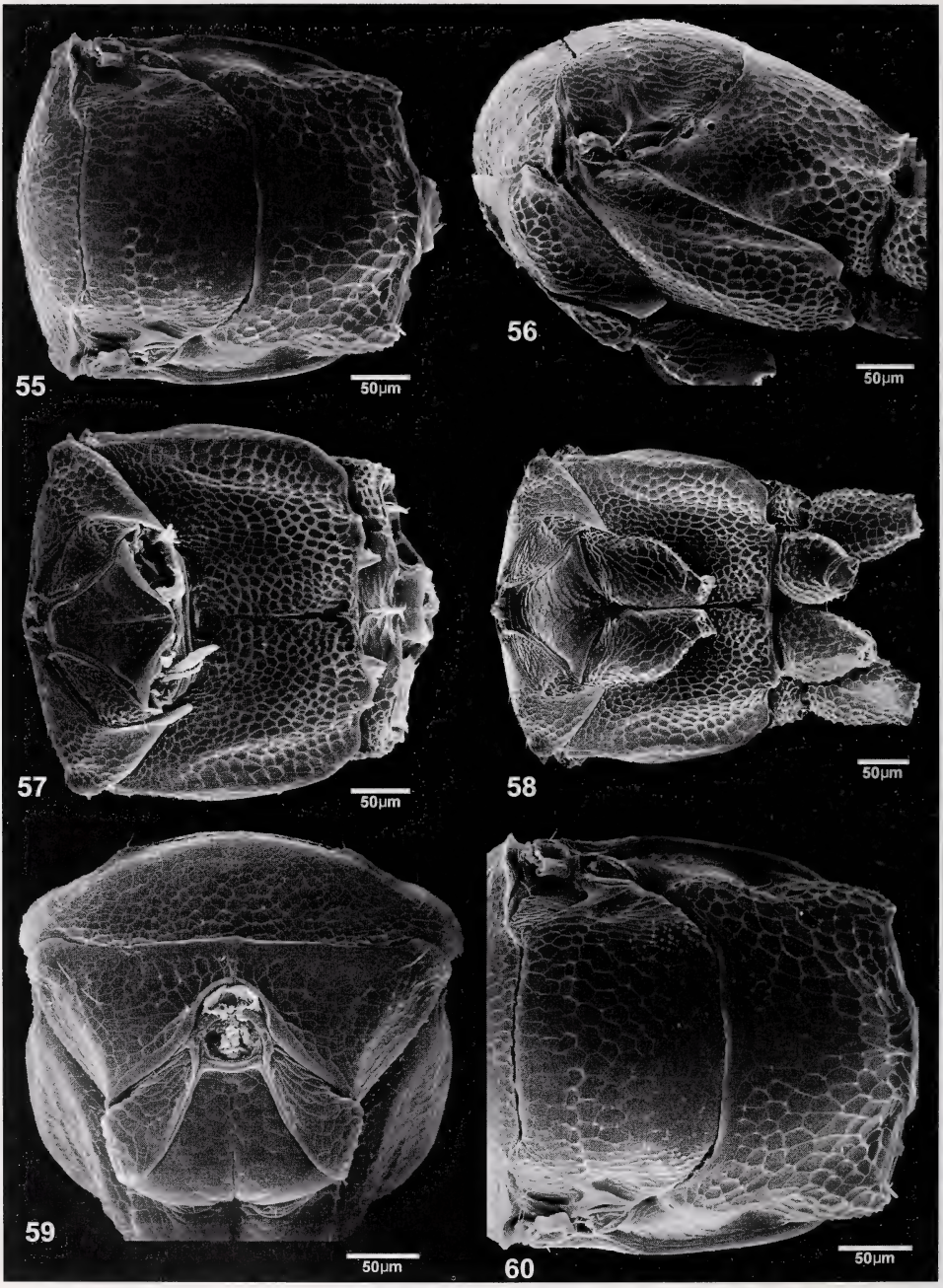
FIGURES 37–42. *Callodicopus* sp. Costa Rica, Guanacaste, Santa Rosa National Park. 37–41, head: 37, dorsal; 38, lateral; 39, anterior; 40, ventral; 41, posterior; 42, mouthparts.



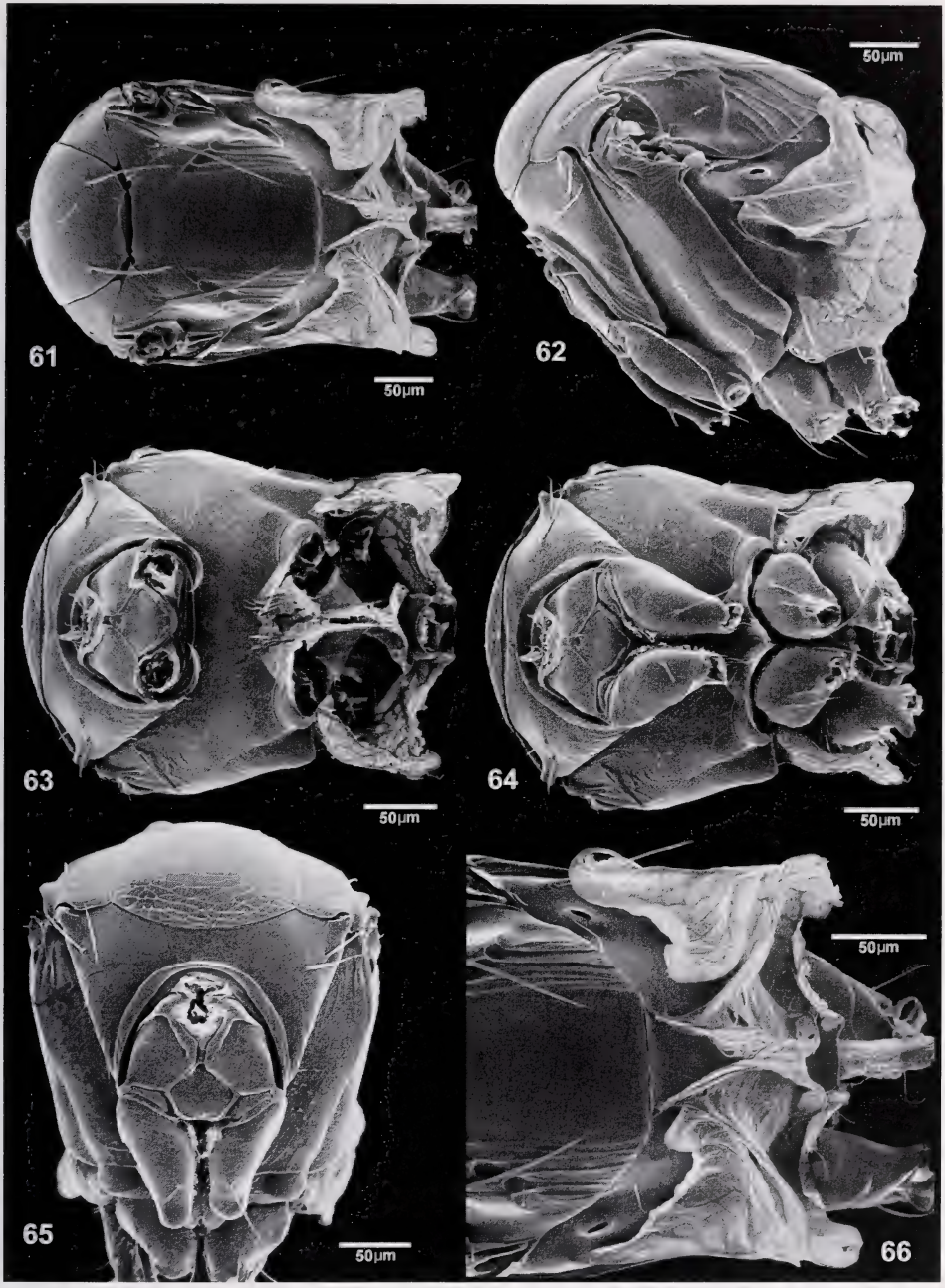
FIGURES 43–48. *Camptopteroides* (*Camptopteroides*) sp. Australia, Queensland, Mt. Lewis. 43–47, mesosoma: dorsal; 44, lateral; 45, 46, ventral, without and with coxae; 47, anterior; 48, propodeum, dorsal.



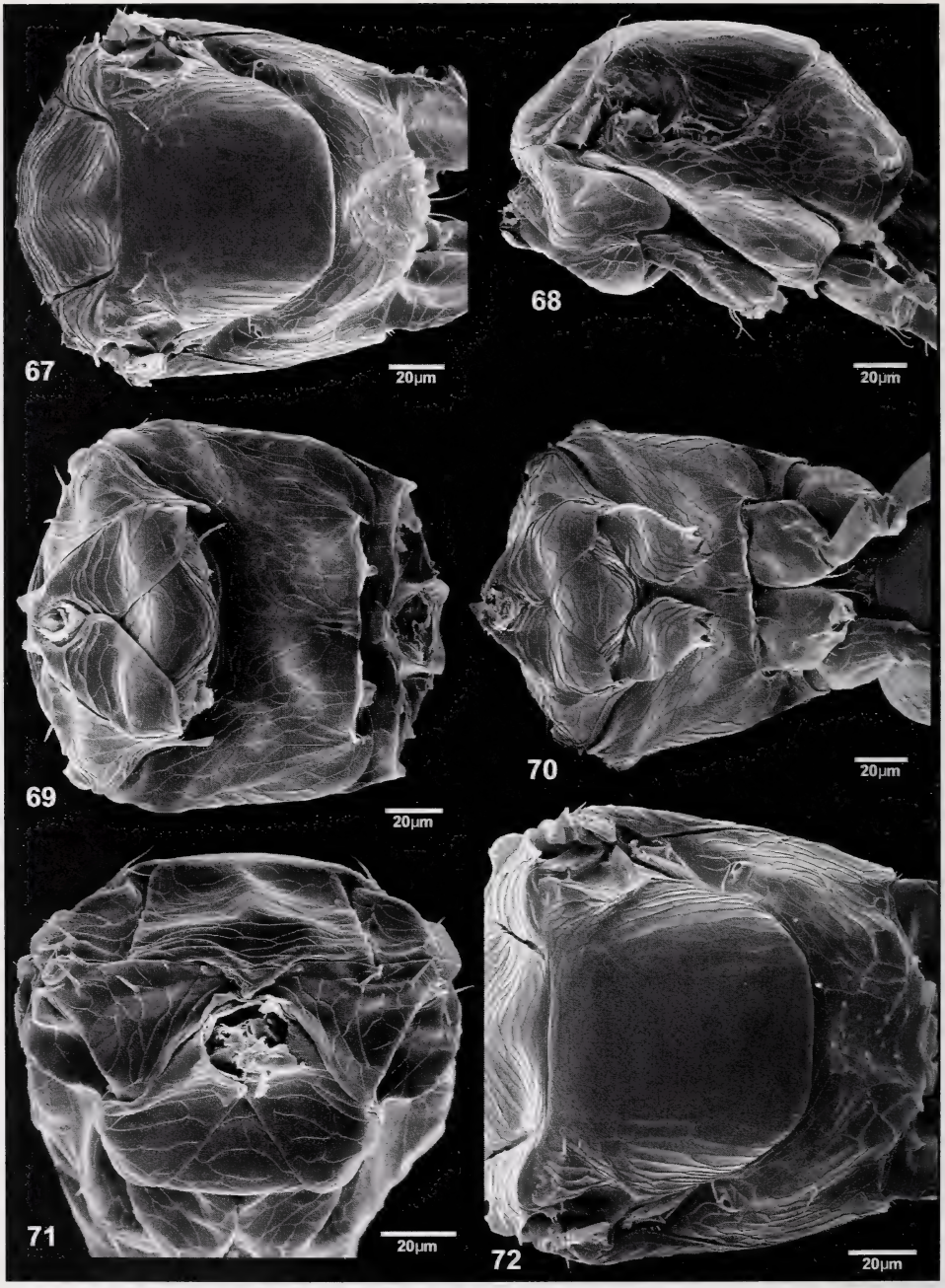
FIGURES 49–54. *Camptopteroides* (*Alalinda*) spp., Costa Rica, Limón and Carthago, and Ecuador, Sucumbios, Sacha Lodge. 49–53, mesosoma: 49, dorsal; 50, lateral; 51, 52 ventral, without and with coxae; 53, anterior; 54, propodeum, dorsal.



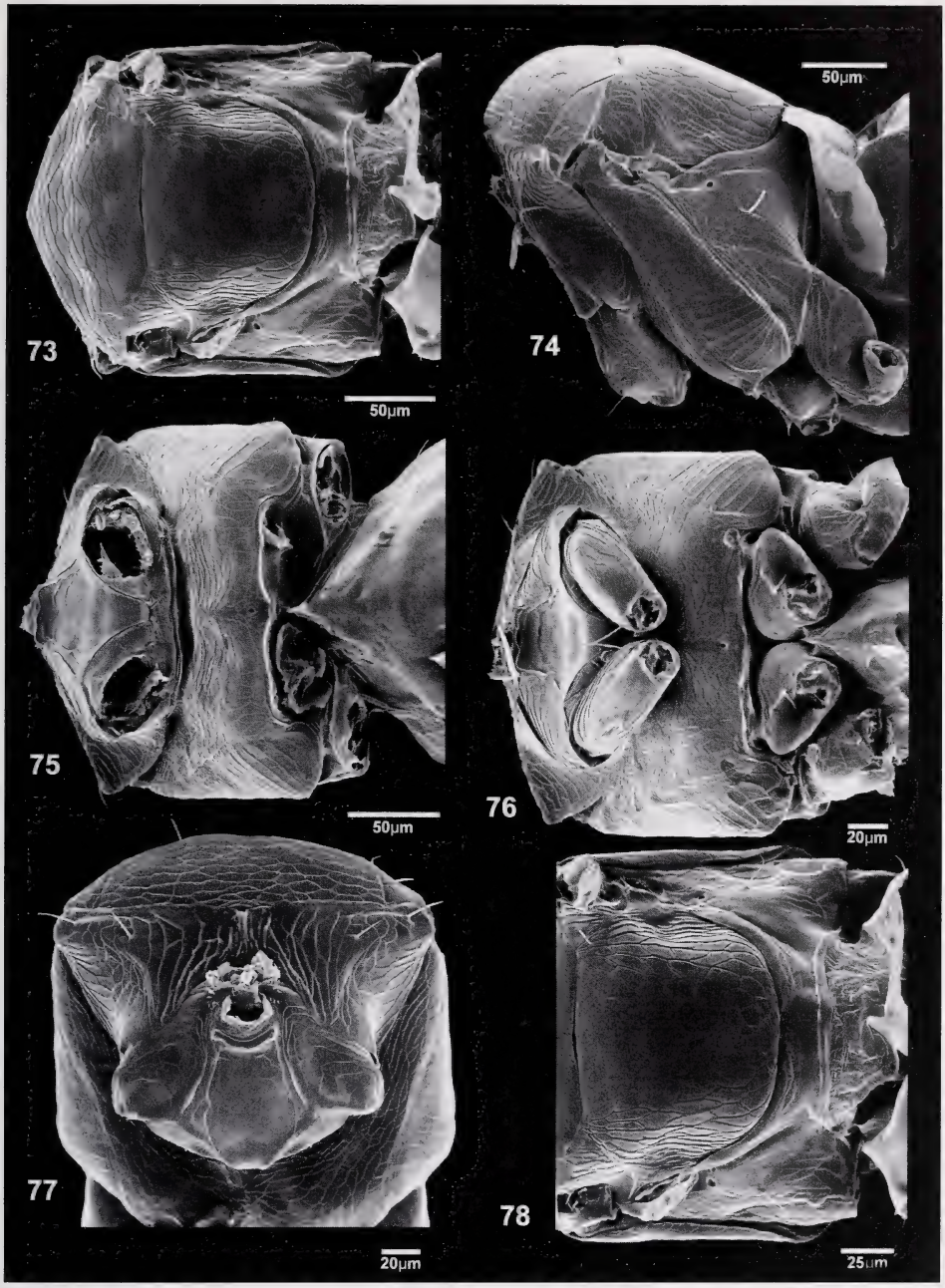
FIGURES 55–60. *Macrocamptoptera metotarsa* (Girault), USA, SC, Pendleton. 55–59, mesosoma: 55, dorsal; 56, lateral; 57, 58, ventral, without and with coxae; 59, anterior; 60, propodeum, dorsal.



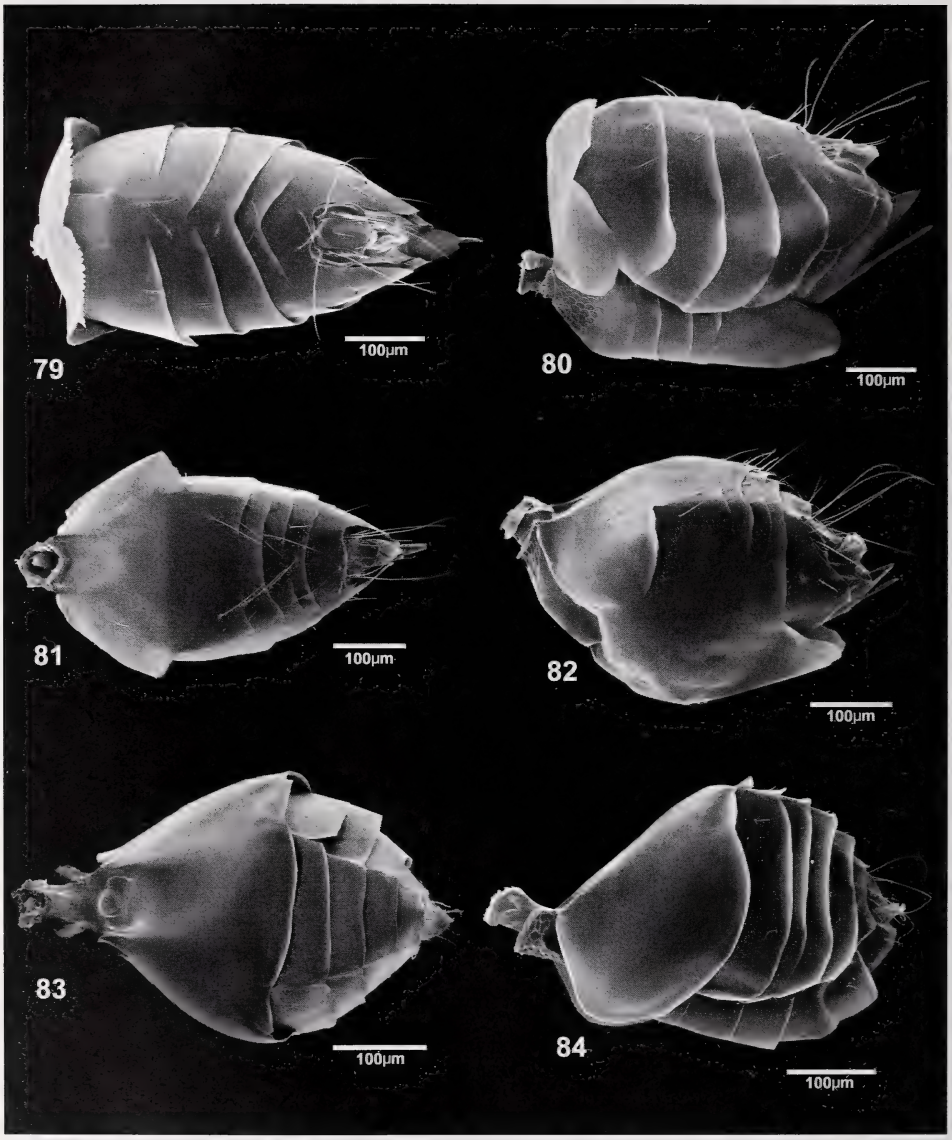
FIGURES 61–66. *Stephanocampta* sp., Ecuador, Napo, Sierra Azul. 61–65: 61, dorsal; 62, lateral; 63, 64, ventral, without and with coxae; 65, anterior; 66, propodeum, dorsal.



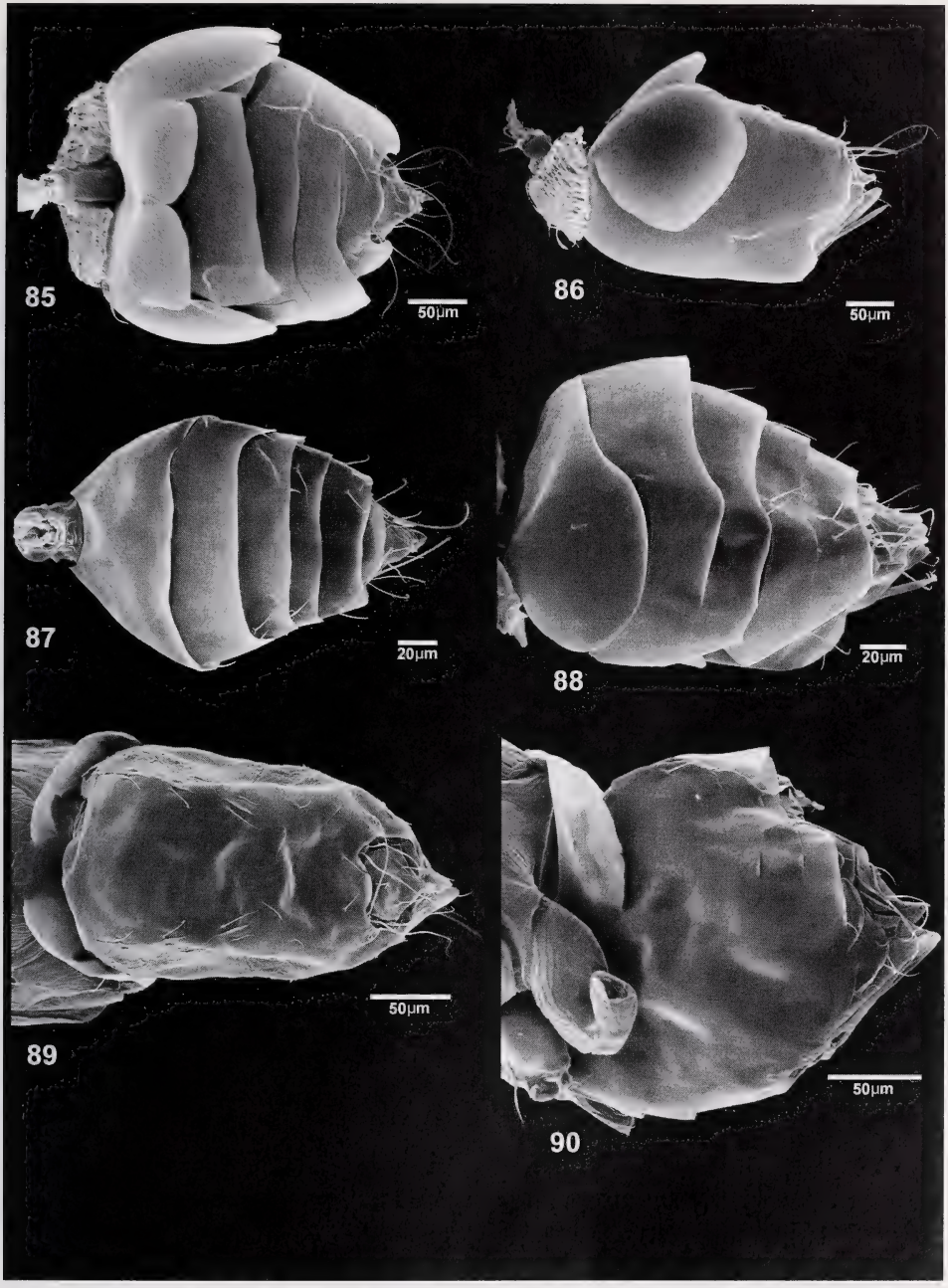
FIGURES 67–72. *Camptoptera* sp. USA, FL, Monroe Co., No Name Key. 67–71, mesosoma: 67, dorsal; 68, lateral; 69, 70, ventral, without and with coxae; 71, anterior; 72, propodeum, dorsal.



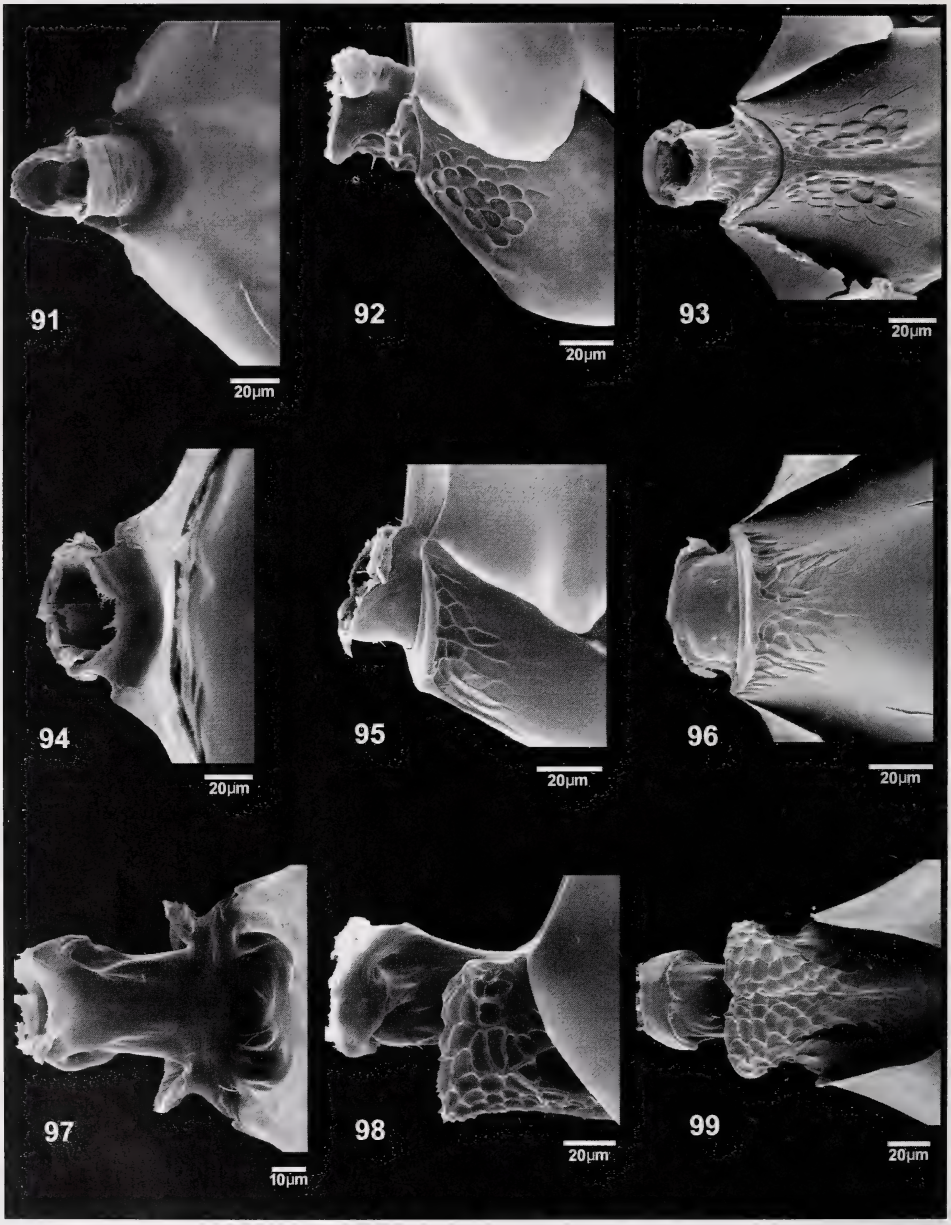
FIGURES 73–78. *Callodicopus* sp. Costa Rica, Guanacaste, Santa Rosa National Park. 73–77: 73, dorsal; 74, lateral; 75, 76, ventral, without and with coxae; 77, anterior; 78, propodeum, dorsal.



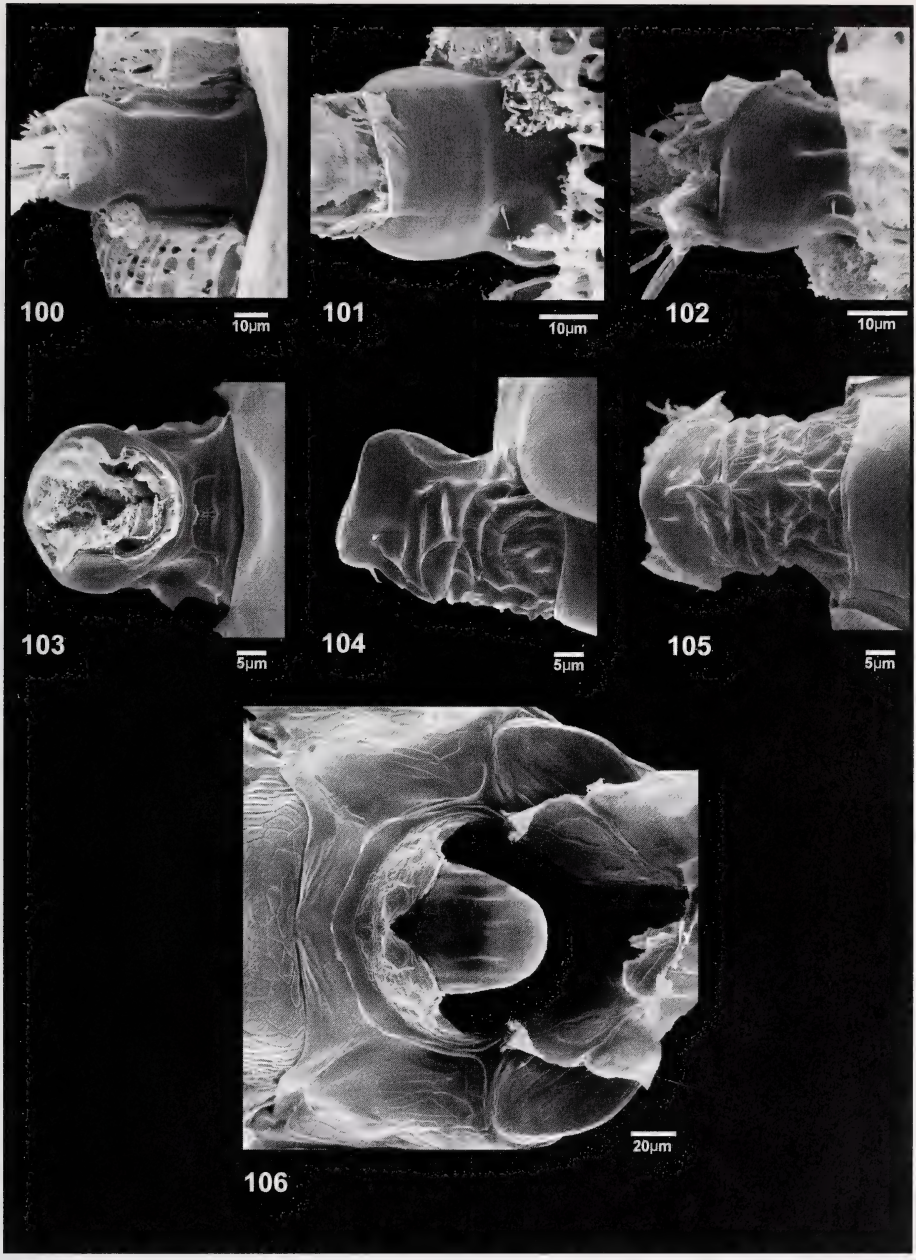
FIGURES 79–84. Metasoma. 79, 80, *Camptopteroides* (*Camptopteroides*), Australia, Queensland, Mt. Lewis. 79, dorsal; 80, lateral. 81, 82, *Camptopteroides* (Alalinda), Costa Rica, Limón, and Ecuador, Sucumbios, Sacha Lodge. 81, dorsal; 82, lateral. 83, 84, *Macrocamptoptera metotarsa* (Girault), USA, SC, Pendleton. 83, dorsal; 84, lateral.



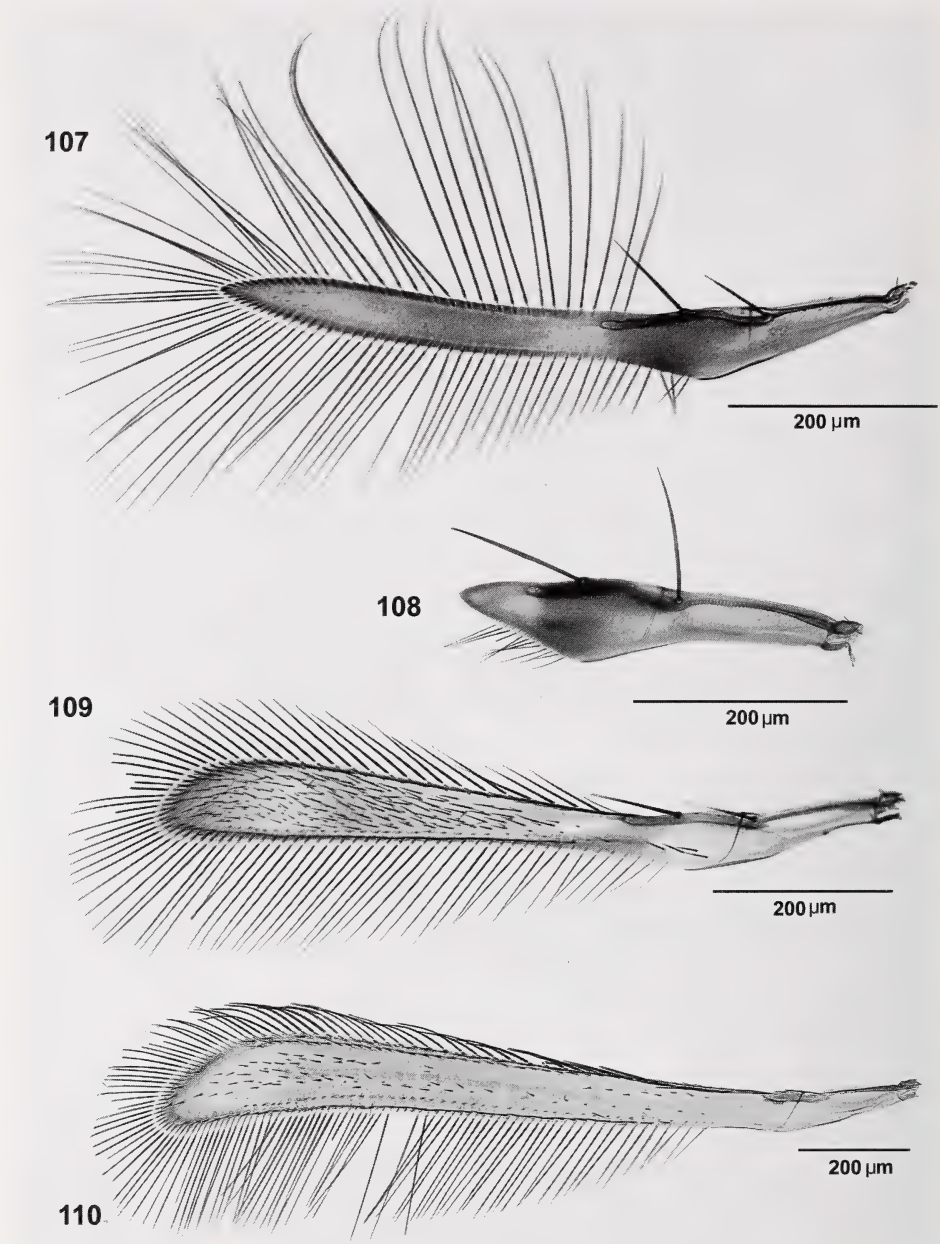
FIGURES 85–90. Metasoma. 85, 86, *Stephanocampta* sp., Ecuador, Napo, Sierra Azul. 85, dorsal; 86, lateral. 87, 88, *Camptoptera* sp. USA, FL, Monroe Co., No Name Key. 87, dorsal; 88, lateral. 89, 90, *Callodicopus* sp. Costa Rica, Guanacaste, Santa Rosa National Park. 89, dorsal; 90, lateral.



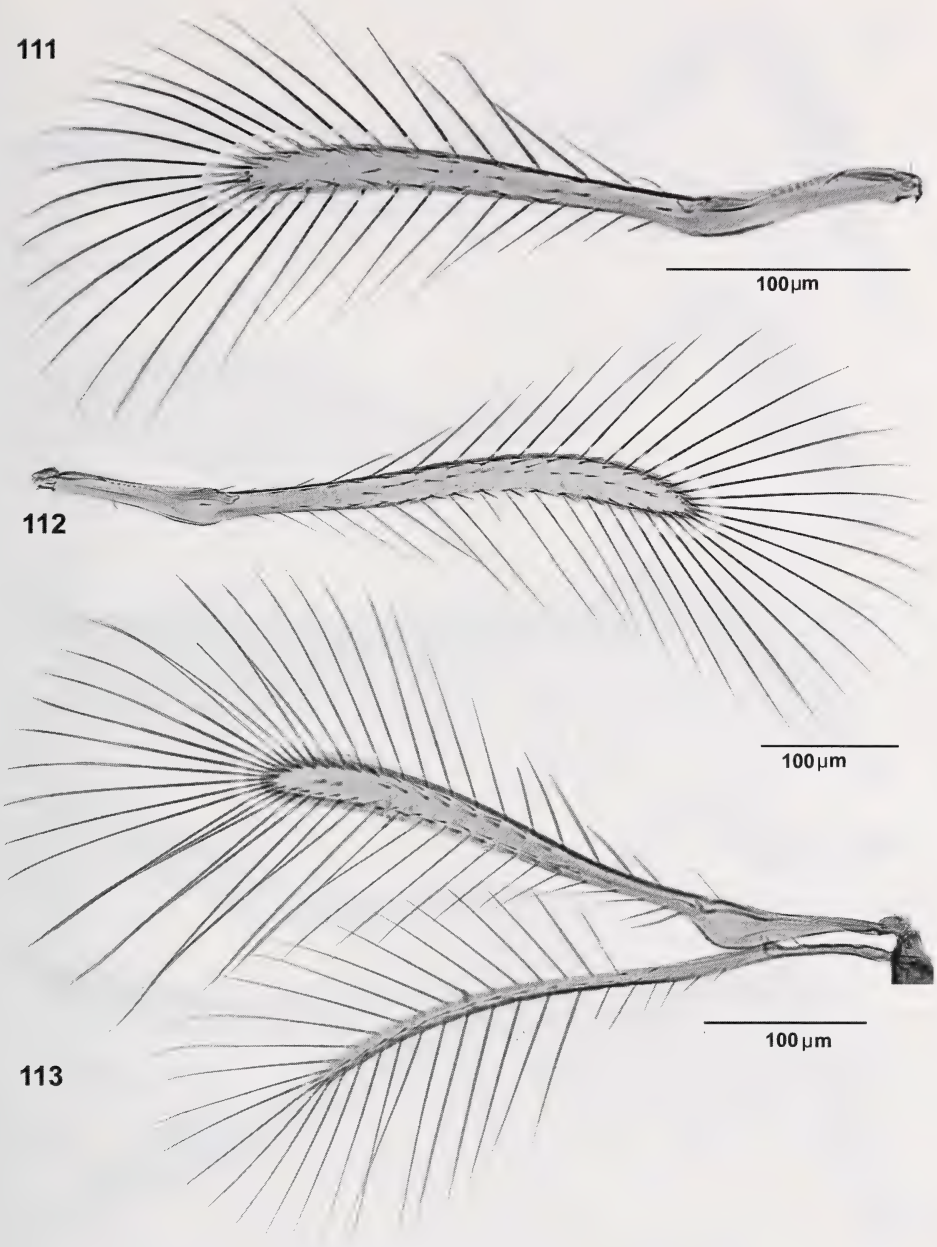
FIGURES 91–99. Gastral petiole. 91–93, *Camptopteroides* (*Camptopteroides*), Australia, Queensland, Mt. Lewis. 91, dorsal; 92, lateral; 93, ventral. 94–96, *Camptopteroides* (*Alalinda*), Costa Rica, Limón. 94, dorsal; 95, lateral; 96, ventral. 97–99, *Macrocamptoptera metotarsa* (Girault), USA, SC, Pendleton. 97, dorsal; 98, lateral; 99, ventral.



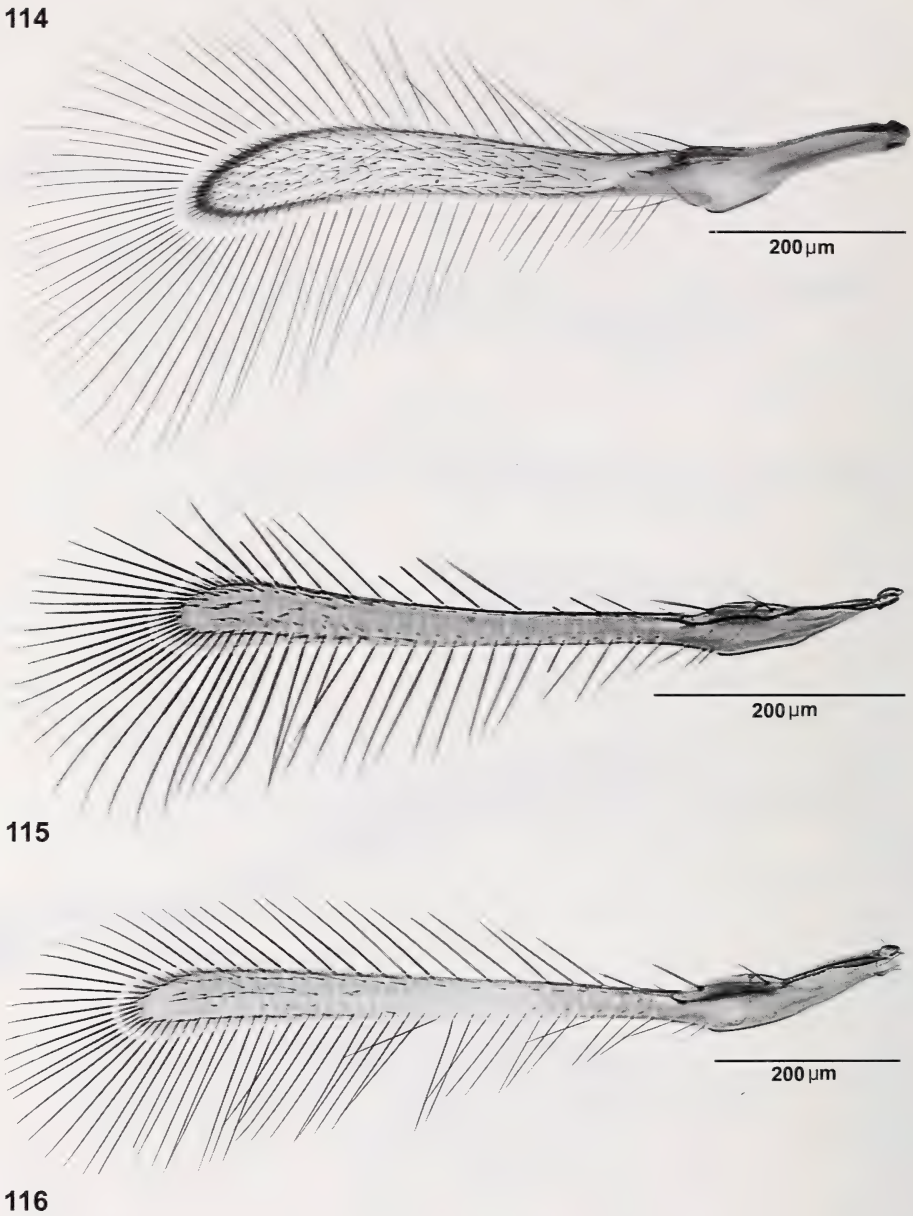
FIGURES 100–106. 100–105, gastral petiole. 100–102, *Stephanocampta* sp., Ecuador, Napo, Sierra Azul. 100, dorsal; 101, lateral; 102, ventral. 103–105, *Camptoptera* sp. USA, FL, Monroe Co., No Name Key. 103, dorsal; 104, lateral; 105, ventral. 106, propodeum, propodeal foramen and apex of mesophgragma, *Callodicopus* sp. Costa Rica, Guanacaste, Santa Rosa National Park.



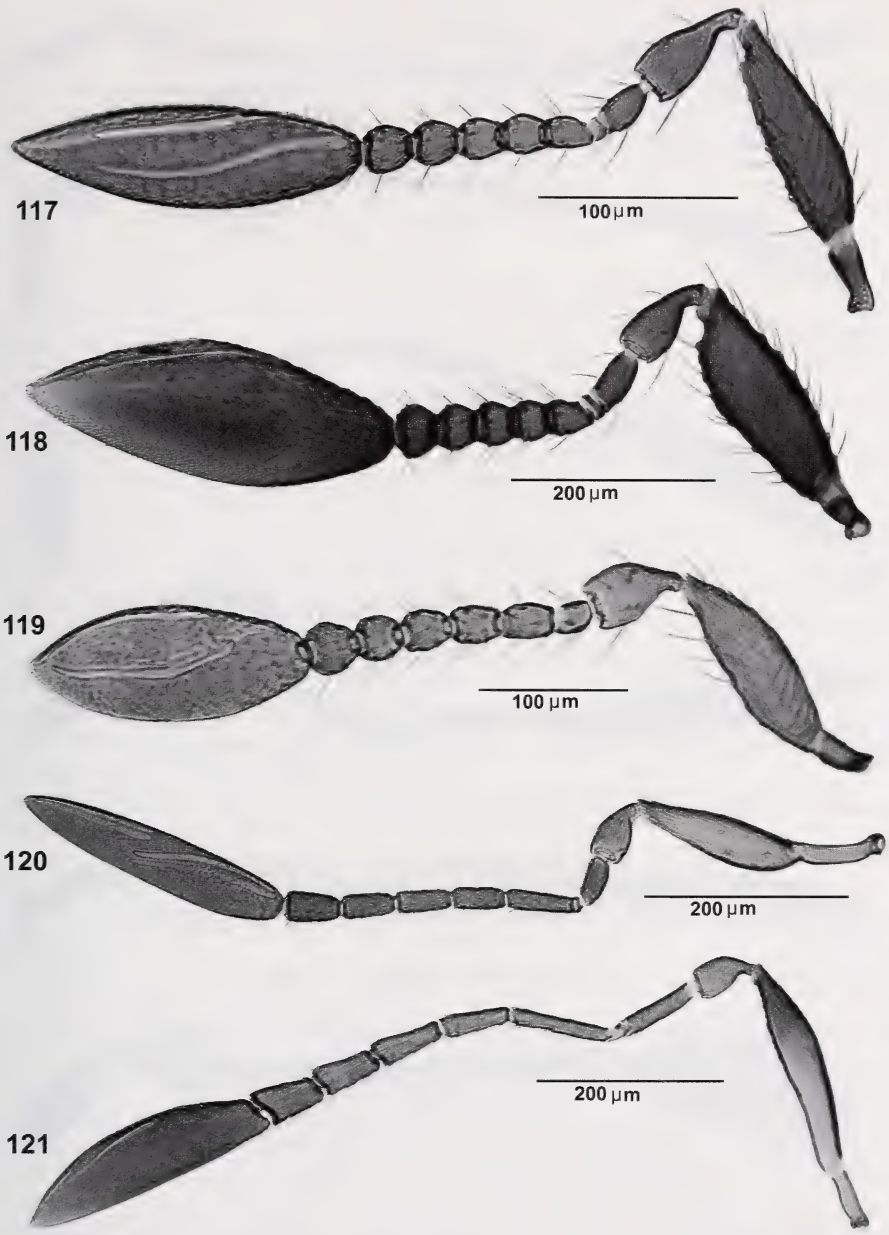
FIGURES 107–110. Forewings. 107, 108: *Camptopteroides* (*Camptopteroides*) spp. ♀, Malaysia, Sabah, Mt. Kinabalu National Park headquarters, macropterous and brachypterous specimens; 109, *Camptopteroides* (*Alalinda*) *dorothea* ♀, PARATYPE; 110, *Macrocamptoptera metotarsa* Girault, USA, SC, Anderson Co., Pendleton.



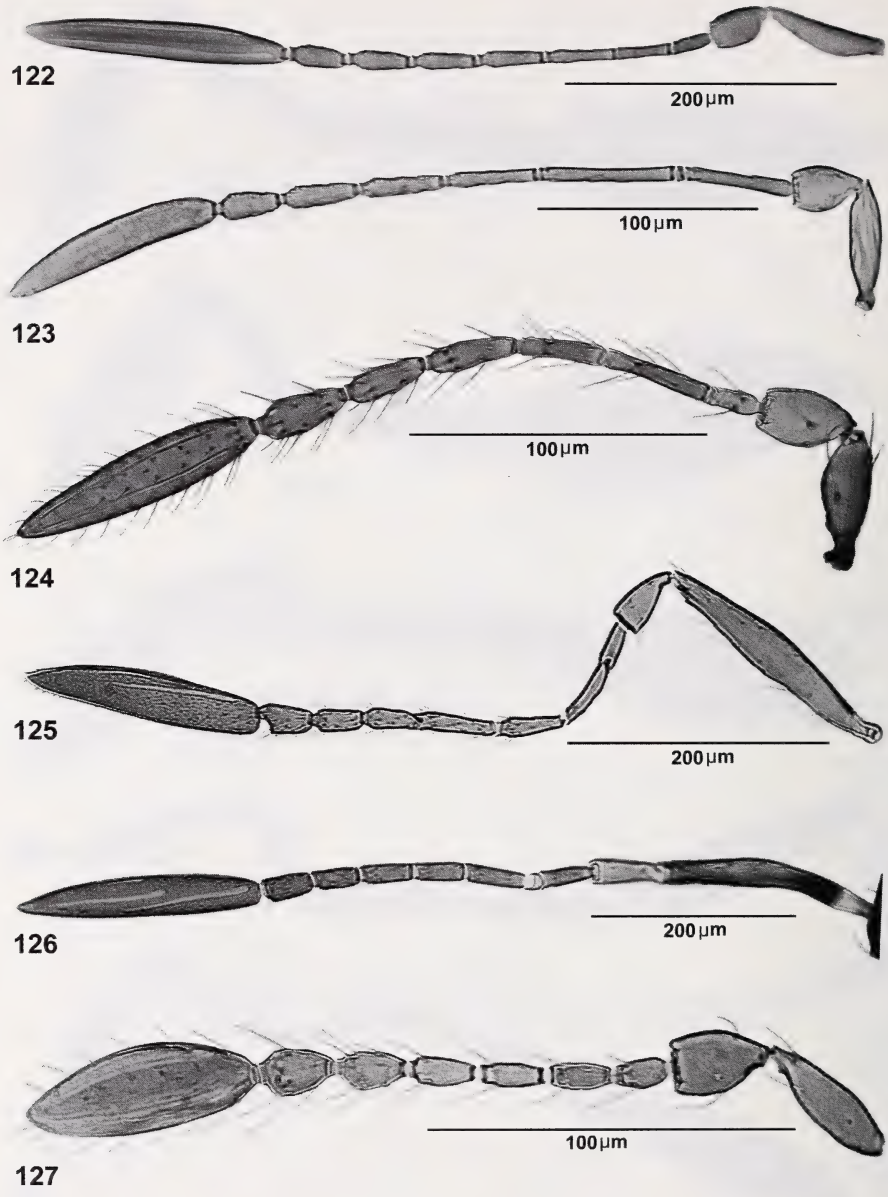
FIGURES 111–113. Wings. 111, *Eofoersteria* sp., USA, FL, Dade Co. Miami Deering Estate Park; 112, *Camptoptera* sp., Austria, Lower Austria, near Hainburg; 113, *Sphegilla* sp., Switzerland, Zurich, Uerlikon.



FIGURES 114–116. Forewings. 114, *Stephanocampta* sp., Costa Rica, Carthago, 4 km N. Cañon Genesis II; 115, *Callodicopus* sp., Costa Rica, Guanacaste, Santa Rosa National Park; 116, *Callodicopus magniclave* (Annecke) ♀, PARATYPE.



FIGURES 117–121. Female antennae. 117, 118, *Camptopteroides* (*Camptopteroides*) spp. ♀, Malaysia, Sabah, Mt. Kinabalu National Park headquarters, from macropterous and brachypterous specimens; 119, *Camptopteroides* (*Camptopteroides*) sp. ♀, Indonesia, Sulawesi, Kotamobagu, Gunung Muajat; 120; *Camptopteroides* (*Alalinda*) *dorothea* ♀, PARATYPE; 121, *Macrocamptoptera metotarsa* Girault, USA, SC, Anderson Co., Pendleton.



FIGURES 122–127. Female antennae. 122, *Stephanocampta* sp., Costa Rica, Carthago, 4 km N. Cañon Genesis II; 123, *Camptoptera* sp., Austria, Lower Austria, near Hainburg; 124, *Sphegilla* sp., Switzerland, Zurich, Uerlikon (clava originally separate, probably dorsal view); 125, *Callodicopus* sp., Costa Rica, Guanacaste, Santa Rosa National Park; 126, *Callodicopus magniclave* (Annecke) ♀ , PARATYPE (dorsal view); 127, *Eofoersteria* sp., USA, FL, Dade Co. Miami Deering Estate Park.

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We thank the curators of the various museums listed in the methods section for loaning material for study, particularly type specimens. K. Bolte, Canadian Forest Service, prepared the scanning electon micrographs, and C. Bhumgara, a Career Edge intern, cleaned the figures and helped compile the plates electronically.

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TAXONOMIC REVIEW OF THE CANADIAN SPECIES OF THE GENUS *MONOTOMA* HERBST (COLEOPTERA: MONOTOMIDAE)

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Abstract *Proc. ent. Soc. Ont.* 130: 67–96

The Canadian species of the genus *Monotoma* Herbst are reviewed. Twelve species are recognized, including three new species, *M. johnsoni* (type locality: Kerrville, Texas), *M. myrmecophila* (type locality: Aweme, Manitoba), and *M. emarginata* (type locality: Ottawa-Kanata, Ontario). The following new synonyms are proposed: *M. fulvipes* Melsheimer, 1844, *M. opaca* Ziegler, 1845, *M. fulvipennis* Motschulsky, 1868, *M. subnigra* Motschulsky, 1868, *M. obsolescens* Casey, 1916, and *M. famelica* Casey, 1916 with *M. picipes* Herbst, 1793; *M. quadraria* Casey, 1916 with *M. testacea* Motschulsky, 1845; *M. parallela* LeConte, 1855 with *M. bicolor* Villa and Villa, 1835; *M. avara* Blatchley, 1928 with *M. arida* Casey, 1916; *M. corpulenta* Motschulsky, 1868 and *M. rhodeana* Casey, 1916 with *M. americana* Aubé, 1837. Lectotypes are designated for *M. fulvipennis* Motschulsky, 1868, *M. subnigra* Motschulsky, 1868, *M. spinicollis* Aubé, 1837, *M. corpulenta* Motschulsky, 1868, *M. producta* LeConte, 1855, *M. famelica* Casey, 1916, *M. quadraria* Casey, 1916, *M. arida* Casey, 1916, and *M. rhodeana* Casey, 1916. The following information is provided for each species treated: citation of original description and synonymy, etymology (for new species only), type material studied, notes about synonymy (if required), recognition, description, distribution, and habitat. A key to the species is provided and important structural features are illustrated.

Résumé *Proc. ent. Soc. Ont.* 130: 67–96

Cet ouvrage comprend une revue des espèces canadiennes du genre *Monotoma* Herbst. En tout 12 espèces sont traitées dont 3 sont nouvelles pour la science: *M. johnsoni* (localité-type: Kerrville, Texas), *M. myrmecophila* (localité-type: Aweme, Manitoba) et *M. emarginata* (localité-type: Ottawa-Kanata, Ontario). On propose la synonymie suivante: *M. fulvipes* Melsheimer, 1844, *M. opaca* Ziegler, 1845, *M. fulvipennis* Motschulsky, 1868, *M. subnigra* Motschulsky, 1868, *M. obsolescens* Casey, 1916 et *M. famelica* Casey, 1916 avec *M. picipes* Herbst, 1793; *M. quadraria* Casey, 1916 avec *M. testacea* Motschulsky, 1845; *M. parallela* LeConte, 1855 avec *M. bicolor* Villa and Villa, 1835; *M. avara* Blatchley, 1928 avec *M. arida* Casey, 1916; *M. corpulenta* Motschulsky, 1868 et *M. rhodeana* Casey, 1916 avec *M. americana* Aubé, 1837. On désigne des lectotypes pour *M. fulvipennis* Motschulsky, 1868, *M. subnigra* Motschulsky, 1868, *M. spinicollis* Aubé, 1837, *M. corpulenta* Motschulsky, 1868, *M. producta* LeConte, 1855, *M. famelica* Casey, 1916, *M. quadraria* Casey, 1916, *M. arida* Casey, 1916 et *M. rhodeana* Casey, 1916. Pour chaque espèce traitée, on donne les informations suivantes: citation de la description originale, **References**

synonymie, étymologie (pour les nouvelles espèces seulement), description du matériel-type étudié, notes sur la synonymie (si nécessaire), diagnose, description, répartition géographique et notes sur l'habitat. Un tableau de détermination des espèces est inclus et les caractères structuraux importants sont illustrés.

Introduction

Herbst proposed the genus *Monotoma* in 1793 for two new species, *M. striata* and *M. picipes*. The first species is now included in the genus *Synchita* Hellwig, 1792 (as a junior synonym of *S. humeralis* Fabricius, 1792) of the family Colydiidae and the second species, *M. picipes*, was designated as the type species of the genus *Monotoma* by Westwood (1838). Since then about 70 species of *Monotoma* have been described worldwide, of which some 40 names are still valid today. Several species have been introduced into various parts of the world through imported stored food products, so the genus could be considered as cosmopolitan.

The genus *Monotoma* has been included for a long time in the family Lathridiidae (Redtenbacher 1849, 1858, 1874; Thomson 1863; Seidlitz 1888 and others) or Cucujidae (Jacquelin du Val 1857; Ganglbauer 1899; Reitter 1911 and others), until it was placed in the family Rhizophagidae (Crowson 1955). Recently, Lawrence and Newton (1995) indicated that the family-group name Monotomidae, proposed by Laporte (1840), has priority over the family-group name Rhizophagidae, proposed by Redtenbacher (1845).

There is little literature dealing with the North American species of *Monotoma*. Horn (1879) published a synopsis of the species; Blatchley (1910) covered the species of Indiana; Casey (1916) described several new species; Hatch (1962) treated the species of the Pacific Northwest; and Downie and Arnett (1996) covered the species of northeastern North America.

Some species are associated with stored food products in Canada and their identification is often difficult using the existing literature. The purpose of this paper is to provide an identification tool for all the species found in Canada. With the exception of two species occurring in southern United States, *M. mucida* LeConte and *M. texana* Horn, this study covers all the described species from North America. Nevertheless, we have seen a number of apparently undescribed species from southern United States.

Materials and Methods

Male genitalia were extracted with fine forceps after the specimens were softened in hot water for 3–5 min. The genitalia were transferred to isopropyl alcohol for several hours, placed in xylene for a few seconds, and mounted in Canada balsam on transparent plastic plates. These structures were studied with an interference contrast microscope. These plastic plates were then subsequently pinned under the corresponding specimens.

The following measurements were taken from ten specimens of each species, using an eyepiece reticle on a stereomicroscope: length of pronotum along midline (L), and maximum width of pronotum excluding the posterior angles (W). Each species description ends with the size range (in millimetres), which is the range of the apparent total body length. This measurement was obtained by visually selecting three or four of the smallest and of the largest specimens and measuring them with a ruler along midline from the tip of the mandibles to the apex of the left elytron.

This study is based on the examination of approximately 3300 specimens borrowed from the following institutions. The name of the curators are listed after the institution addresses.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, United States. Lee H. Herman.
BMNH	Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, England. Martin J.D. Brendell.
CCCH	Claude Chantal Collection, 302 Gabrielle-Roy, Varennes, Québec J3X 1L8, Canada.
CDAE	California State Collection of Arthropods, Department of Food and Agriculture, 1220 N Street, Sacramento, California 95814, United States. Fred G. Andrews.
CNCI	Canadian National Collection of Insects, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Ottawa, Ontario K1A 0C6, Canada.
CPPA	Pierre Paquin Collection, 11629 Des Violettes, Montréal-Nord, Québec H1G 4N1, Canada.
CUIC	Department of Entomology, Cornell University, Ithaca, New York 14850, United States. James K. Liebherr.
FMNH	Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, United States. Alfred F. Newton.
FSCA	Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, P.O. Box 147100, Gainesville, Florida 32614, United States. Michael C. Thomas.
INHS	Section of faunistic surveys and insect identification, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, United States. Kathryn C. McGiffen.
LSUC	Louisiana State University Insect Collection, Department of Entomology, Louisiana State University, Baton Rouge, Louisiana 70803, United States. Vicky L. Moseley.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, United States. David G. Furth.
MHNP	Muséum National d'Histoire Naturelle, 45 rue Buffon, F-75005 Paris, France. Nicole Berti.
MMUM	The Manchester Museum, The University, Manchester M13 9PL, England. Colin Johnson.
NHDE	Entomological Museum, Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824, United States. Donald S. Chandler.
ORUM	Collection Ouellet-Robert, Département de biologie, Université de Montréal, Case Postale 6128, Montréal, Québec H3C 3J7, Canada. Louise Cloutier.
OSUC	Department of Entomology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210, United States. Charles A. Triplehorn.
PURC	Department of Entomology, Purdue University, Lafayette, Indiana 47907, United States. Arwin Provonsha.
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USNM	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560, United States. James Pakaluk.
ZMUM	Zoological Museum, Moscow State University, Moscow 103009, Russia. Nikolai B. Nikitsky.

Terms for structures

The terms we use for external structures should be well known to coleopterists. However, the male genitalia of *Monotoma* have been little studied and will be discussed briefly. The tegmen is in a dorsal position and scoop-shaped; its apical margin is more or less rounded in most species, notched in others. The median lobe is rather short, broad, flat, slightly curved, and fits into the depression of the tegmen; it consists of two laminae that are fused basally, a ventral one, notched at middle in most species, and a dorsal one, truncate at the middle in most species (see Fig. 16).

Genus *Monotoma* Herbst, 1793

Monotoma Herbst 1793: 22. Type species: *Monotoma picipes* Herbst, 1793, subsequent designation by Westwood (1838: 13). Aubé (1837: 454); Redtenbacher (1849: 23, 202; 1858: lxxxiv, 377; 1874: xci, 413); Lacordaire (1854: 434); Jacquelin du Val (1857: 197); Wollaston (1857: 67; 1871: 239); LeConte (1861: 86); Thomson (1863: 211); Motschulsky (1868: 196); Reitter (1876: 297; 1884: 272; 1901*a*: 193; 1901*b*: 3; 1911: 42); Horn (1879: 258); LeConte and Horn (1883: 155); Seidlitz (1872: 41 [Gattungen]; 1888: 60 [Gattungen]; 1889: 60 [Gattungen]); Fowler (1889: 270); Acloque (1896: 218); Everts (1899: 562); Ganglbauer (1899: 571); Stierlin (1900: 565); Grouvelle (1908*b*: 493); Blatchley (1910: 667); Kuhnt (1912: 503); Jacobson (1915: 898); Casey (1916: 88); Hansen (1950: 146); Arnett (1962: 768); Hatch (1962: 251); Kuschel (1979: 45); Ślipiński (1981: 6); Nikitsky (1986: 1625); Sengupta (1988: 22); Downie and Arnett (1996: 985–986).

Diagnosis. Adults of *Monotoma* are easily recognized among North American members of the family Monotomidae by the coarse, subcontiguous punctures on the head dorsally and on the pronotum (except in *M. longicollis* Gyllenhal), by the rows of paired punctures on the elytra, as well as by the protruding anterior angles of the pronotum (less so in *M. quadrifoveolata* Aubé).

Description. (see Lawrence (1982) and Sengupta (1988) for family character states). **Shape**. Elongate, not depressed, covered with moderately dense setae, 1.4–3.2 mm. **Head**. Neck with short but distinct constriction; temples less than twice length of longitudinal diameter of eyes. Eyes well developed. Antennomere 1 globular; antennomere 2 smaller than antennomere 1; antennomere 3 slightly elongate; antennomeres 4–8 short, subequal; antennomere 9 slightly larger than antennomere 8; antennomeres 10–11 more or less fused, much larger than antennomere 9, forming antennal club. Antennal cavities absent. Gular region anteriorly with transverse, semicircular carina joining maxillary foveae. Labial and maxillary palpomeres 2 larger than remaining palpomeres. **Prothorax**. Pronotum subquadrate to elongate (less than 1.3 times as long as wide), in most species with large, more or less subcontiguous punctures; lateral sides with indentations, each carrying one seta; anterior angles prominent in most species; base with pair of shallow foveae. Fore coxal cavities rounded; hind coxal cavities widely separated. **Legs**. Fore trochantins hidden. Tarsal formula 5-5-4 in males, 5-5-5 in females. **Elytra**. Setigerous punctures paired, with seta between them, aligned in longitudinal rows (though more or less confused anteriorly and posteriorly). **Abdomen**. First visible sternite longer than remaining sternites, without coxal lines; visible sternites 2–4 subequal, short. **Male genitalia**. Median lobe short, broad, flattened; tegmen larger than median lobe.

Sexual Dimorphism. Sexes are easily separated by the number of visible abdominal tergites beyond the apex of the elytra. Males have two visible tergites, females one. Some species show sexually dimorphic characters on the front tibia. In the males, the medial side of the front tibia is slightly curved apically and possesses minute spinulae. In females of two species, the posterior

dorsal margin of the head bears a small, median projection. In addition to the above characters, the tarsal formula is different, 5-5-4 in males, 5-5-5 in females.

Monophyly and phylogenetic relationships. The enlarged labial and maxillary palpomeres 2, the paired setigerous punctures on the elytra, and the protruding anterior angles of the pronotum (less so in *M. quadrifoveolata*) are likely autapomorphic states for members of *Monotoma* (see Sengupta's (1988) review of the family) and suggest that the genus is monophyletic.

The general habitus of adults of *Monotoma* is readily different from the habitus of other members of Monotomidae and Sengupta (1988) proposed the tribe Monotomini for *Monotoma*. Until the phylogenetic relationships of the genera of Monotomidae are investigated, the systematic position of the genus *Monotoma* will remain unsettled.

Biology. Little is known about the bionomics of members of *Monotoma*. It is generally accepted that the adults are mould feeders. They mainly occur in decaying vegetable matter, and are often found in man-made habitats such as compost heaps and haystacks (Peacock 1977: 2). Some species also occur in stored food products (Bousquet 1990). The three species of the subgenus *Gyrocecis* Thomson live in nests of the ant genus *Formica* Linné. Gut contents of larvae of *M. producta* LeConte collected in New Hampshire revealed that they feed on the spores of two species of Fungi Imperfecti (Chandler 1983).

Larvae. To date only the larva of *Monotoma producta* has been described and figured (Chandler 1983). Peacock (1977) presented a brief description of the genus based on larvae of *M. brevicollis* Aubé and *M. picipes*.

Distribution. Endemic species of *Monotoma* are known from Europe, Asia, North Africa, Madagascar, North America, and Central America. Some species have been introduced in various parts of the world and the genus could be considered as subcosmopolitan.

Note on subgenera. Besides the nominotypical subgenus, the genus *Monotoma* includes two subgenera: *Monotomina* Nikitsky, 1986 for *M. quadrifoveolata* Aubé, and *Gyrocecis* Thomson, 1863 with *M. angusticollis* Gyllenhal, *M. conicicollis* Guérin-Méneville, and *M. myrmecophila* Bousquet and Laplante. These subgenera were proposed because their members differ readily in their external structures from those of other species of the genus. However, we have seen other species that are structurally as distinct as these species. Until a cladistic analysis of the species of *Monotoma* is completed, we prefer not to use the current subgeneric arrangement.

Note on nomenclature. The name *Monotoma* was originally proposed in 1793 by both Herbst and Panzer. The first author included *M. striata* Herbst, 1793 and *M. picipes* Herbst, 1793 in the genus and the second author included *M. crenata* (Fabricius, 1775). As we have found no information relevant to a precise publication date of the works of Herbst and Panzer, we must assume that the two names were published simultaneously, the last day of the year (ICZN, 1985, Art. 21(c)). To promote stability, *Monotoma* Herbst, 1793 is here regarded as a valid name, with *Monotoma picipes* Herbst, 1793 as the type species, and *Monotoma* Panzer, 1793 (type species: *Tritoma crenata* Fabricius, 1775 by monotypy) as an objective synonym of *Bitoma* Herbst, 1793 (type species: *Tritoma crenata* Fabricius, 1775, subsequent designation by Latreille 1810: 431). Both *Bitoma* Herbst, 1793 and *Monotoma* Panzer, 1793 were published simultaneously and *Bitoma* Herbst is here regarded as the valid name. In summary, *Monotoma* Panzer, 1793 is regarded as a junior homonym of *Monotoma* Herbst, 1793 and a junior objective synonym of *Bitoma* Herbst, 1793.

Checklist of Species Treated

1. *Monotoma longicollis* (Gyllenhal, 1827)
2. *Monotoma picipes* Herbst, 1793
3. *Monotoma spinicollis* Aubé, 1837
4. *Monotoma johnsoni* Bousquet and Laplante, **n.sp.**
5. *Monotoma quadrifoveolata* Aubé, 1837
6. *Monotoma producta* LeConte, 1855
7. *Monotoma myrmecophila* Bousquet and Laplante, **n.sp.**
8. *Monotoma testacea* Motschulsky, 1845
9. *Monotoma bicolor* Villa and Villa, 1835
10. *Monotoma arida* Casey, 1916
11. *Monotoma americana* Aubé, 1837
12. *Monotoma emarginata* Bousquet and Laplante, **n.sp.**

Key to the species of *Monotoma* in Canada and adjacent parts of USA

1 Pronotum distinctly wider anteriorly (Fig. 2). Pronotum with small shallow punctures, irregularly spaced, not contiguous ..... *M. longicollis* (Gyllenhal)
– Pronotum more or less parallel-sided or wider posteriorly (Figs. 3–11). Pronotum with large, deep, contiguous or subcontiguous punctures 2

2 Frons with 2 deep, longitudinal impressions (Fig. 3) ..... *M. picipes* Herbst
– Frons without longitudinal impressions 3

3 Anterior angles of pronotum each produced in form of a large acute tooth (Fig. 4) 4
– Anterior angles of pronotum at most with rounded or blunt nodiform projections 5

4 Pronotum with anterior angles usually projected latero-anteriorly (Fig. 4). Aedeagus as in Fig. 14 ..... *M. spinicollis* Aubé
– Pronotum with anterior angles usually projected laterally (Fig. 24). Aedeagus as in Fig. 23 ..... *M. johnsoni* **n.sp.**

5 Pronotal disc with 4 deep foveae, joined in pairs on each side to form 2 longitudinal furrows (Fig. 5) ..... *M. quadrifoveolata* Aubé
– Pronotal disc with 2, usually shallow, foveae in posterior half, rarely with 2 very shallow impressions in anterior half (not connected to basal foveae) 6

6 Pronotum elongate (ratio L/W usually > 1.18), with extremity of anterior angles blunt (Fig. 6) ..... *M. producta* LeConte
– Pronotum usually less elongate (ratio L/W < 1.15), with extremity of anterior angles rounded (Figs. 7–11) 7

7 Temples relatively long, 0.5–0.8 times length of longitudinal diameter of eye (Figs. 7–9) .. 8
– Temples relatively short, about 0.3 times length of longitudinal diameter of eye (Figs. 10–11) 10

8 Setae on head and pronotum short, wide, more or less recumbent. Pronotum with sides divergent posteriorly (Fig. 7). Antennomere 3 slightly shorter than antennomere 2 ..... *M. myrmecophila* **n.sp.**
– Setae on head and pronotum elongate, narrow, suberect. Pronotum with sides more or less parallel to slightly rounded posteriorly (Figs. 8–9). Antennomere 3 as long as antennomere 2 9

9 Body dorsally more or less uniformly reddish. Pronotum with sides slightly sinuate to parallel, anterior angles slightly protruding (Fig. 8); disc rather flat, with 2 more or less distinct impressions on anterior half ..... *M. testacea* Motschulsky
– Head and pronotum reddish brown to piceous, distinctly darker than elytra. Pronotum with sides usually rounded, anterior angles more protruding (Fig. 9); disc rather convex, without impressions on anterior half ..... *M. bicolor* Villa and Villa

10 Abdomen with 2 exposed tergites..... (♂♂) 11
– Abdomen with 1 exposed tergite ..... (♀♀) 13

11 Last visible abdominal sternite with large, median, oval, finely granulate depression. Pronotum slightly elongate (1.10–1.15 times as long as wide) ..... *M. arida* Casey
– Last visible abdominal sternite at most with small, shallow, relatively smooth depression. Pronotum subquadrate (1.00–1.07 times as long as wide) 12

12 Tegmen shallowly notched at apex (Fig. 21) ..... *M. americana* Aubé
– Tegmen markedly notched at apex (Fig. 22) ..... *M. emarginata* **n.sp.**

13 Pronotum slightly elongate (1.10–1.15 times as long as wide) ..... *M. arida* Casey
– Pronotum subquadrate (1.00–1.07 times as long as wide) 14

14 Posterior margin of head with small, hornlike, median projection (Fig. 11). Last visible abdominal sternite smooth ..... *M. americana* Aubé
– Posterior margin of head without median projection. Last visible abdominal sternite with small protuberance in most specimens ..... *M. emarginata* **n.sp.**

Monotoma longicollis (Gyllenhal, 1827)

(Figs. 2, 12)

Cerylon longicolle Gyllenhal 1827: 635. Type locality: «Sparrsätra Westrogothiae» and «Smolandia». *Monotoma longicollis*: Aubé (1837: 467); Redtenbacher (1858: 377; 1874: 414); Thomson (1863: 212); Seidlitz (1872: 165; 1888: 241; 1889: 256); Reitter (1877: 6; 1901*a*: 197; 1901*b*: 7; 1911: 43); Horn (1879: 261); Fowler (1889: 271, 274); Acloque (1896: 219); Everts (1899: 564; 1922: 253); Ganglbauer (1899: 577); Stierlin (1900: 567); Grouvelle (1908*a*: 21); Blatchley (1910: 669); Kuhnt (1912: 506); Hansen (1950: 147, 151); Hatch (1962: 252); Vogt (1967: 85); Peacock (1977: 12); Kuschel (1979: 45); Ślipiński (1981: 8); Nikitsky (1986: 1627); Milander (1992: 70); Otero and Días-Pazos (1994: 103); Downie and Arnett (1996: 987).

Diagnosis. This species is easily separated from the other taxa treated by the shape of the pronotum, which is wider anteriorly and narrowed posteriorly, and by the shallow, rather small punctures on the head and pronotum.

Description. **Colouration**. Body dorsally more or less uniformly reddish brown to piceous. **Pubescence**. Setae on dorsum of body elongate, narrow, most of those on pronotum and elytra recumbent. **Punctation**. Frons and pronotum with rather small, shallow, more or less dense punctures, often placed in groups of 2 or 3, particularly on disk of pronotum. Metasternum posteromedially and first visible sternite medially with very fine, almost imperceptible punctuation. **Head** (Fig. 2). Frons without deep longitudinal impressions; median area not raised. Female without projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, more or less rounded, not angulate. Eyes proportionally large; temples short, length 0.3–0.4 times that of longitudinal diameter of eyes, more or less divergent and somewhat acutely produced posteriorly. **Thorax**. Pronotum (Fig. 2) elongate, 1.2–1.3 times as long as wide, widest at level of anterior angles; sides tapered toward base; lateral indentations fine; anterior angle slightly protruding, its extremity rounded or blunt; posterior angle indistinct; disc without impressions on anterior half in most specimens (a few specimens seen with 2 very shallow impressions); surface between punctures dull, with isodiametric microsculpture. **Elytra**. Rows of setigerous punctures more confused than in other species treated, especially in apical half. **Abdomen**. Male first visible abdominal sternite without median depression; last visible abdominal sternite simple. **Male genitalia** (7 specimens dissected) (Fig. 12). Ventral lamina emarginate medially; dorsal lamina narrowly rounded medially; tegmen with extremity more or less rounded.

Length of body: 1.4–1.9 mm.

Distribution. This species has been reported from Europe, Caucasus, Japan, west Africa, Australia, New Zealand, and America (Hetschko 1930; Nikitsky 1986). The species has been accidentally introduced in North America. In the United States it is known from Alabama, Arizona, Connecticut, District of Columbia, Florida, Illinois, Indiana, Maine, Massachusetts, Minnesota, Missouri, Nevada, New Hampshire, North Carolina, Oklahoma, Vermont, Wisconsin. We have seen Canadian specimens from the following localities: **Newfoundland**. Portugal Cove, 19.VII.1981 (CNCI) 3. **New Brunswick**. Kouchibouguac Nat. Pk., 21.IX.1977, Campbell & Smetana (CNCI) 3; idem, 12.IX.1977, G.A. Calderwood (CNCI) 1. **Québec**. Montréal 18.IV., 25.IV., J. Ouellet (ORUM) 2; idem, 2.IX.1973, E.J. Kiteley (CNCI) 1. Frelighsburg, 21.V.1985, N.J. Bostanian (CNCI) 1. Montebello 29.VII.37, J. Ouellet (ORUM) 1. La Trappe 28.V.44, 14.VI.44, 29.VI.44, J. Ouellet (ORUM) 3. 112 km N La Sarre, 7–14.IX.1997, P. Paquin (CPPA) 1. 122 km N La Sarre, 7–14.IX.1997, P. Paquin (CPPA) 1. Lac Duparquet, 17–24.VII.1994, 25.VIII.–1.IX.1996, 1–8.IX.1996, P. Paquin (CPPA) 3. Lac Labyrinthe, 1–8.IX.1996, P. Paquin (CPPA) 1. **Ontario**. Ottawa-Kanata, 25.V.1979, 9.VII.1979, A.& Z. Smetana (CNCI) 5. **Saskatchewan**. Bounty, 2.XI.53 (CNCI) 3. Thrasher, 1.XII.1953, D.B. Waddell (CNCI) 6. Zealandia, 25.V.1953, H. McDonald (CNCI) 1. Sovereign, 27.VII.1954, D.B. Waddell (CNCI) 1. **Alberta**. Calgary, 27.VIII.1981, B.F. & J.L. Carr (CNCI) 1.

Habitat. Some of the specimens studied were collected in grass piles and in stored wheat.

Monotoma picipes Herbst, 1793

(Figs. 1, 3, 13)

Monotoma picipes Herbst 1793: 24. Type locality not mentioned. Aubé (1837: 458); Redtenbacher (1849: 203; 1858: 378; 1874: 415); Thomson (1863: 211); Reitter (1877: 6; 1884: 272; 1901*a*: 194; 1901*b*: 4; 1911: 43); Seidlitz (1872: 165; 1888: 240; 1889: 255); Horn (1879: 259); Fowler (1889: 271, 273); Acloque (1896: 219); Everts (1899: 563; 1922: 253); Ganglbauer (1899: 576); Stierlin (1900: 567); Blatchley (1910: 668); Kuhnt (1912: 506); Hansen (1950: 147, 151); Hatch (1962: 251); Vogt (1967: 85); Kuschel (1979: 46); Ślipiński (1981: 9); Nikitsky (1986: 1628); Milander (1992: 71); Otero and Días-Pazos (1994: 101); Downie and Arnett (1996: 987).

Lyctus picipes: Paykull (1800: 331).
Cerylon picipes: Gyllenhal (1813: 417).
Monotoma fulvipes Melsheimer 1844: 111. Type locality: "Pennsylvania" [**new synonymy**].
Monotoma opaca Ziegler 1845: 271. Type locality: "Pennsylvania" [**new synonymy**].
Monotoma foveatum LeConte 1855: 305. Type locality: "Ohio". Synonymy established by Horn (1879: 259).
Monotoma fulvipennis Motschulsky 1868: 199. Type locality: "Amérique boréale" [**new synonymy**].
Monotoma subnigra Motschulsky 1868: 199. Type locality: "Amérique du Nord" [**new synonymy**].
Monotoma obsolescens Casey 1916: 88. Type locality: "District of Columbia" [**new synonymy**]. Downie and Arnett (1996: 987).
Monotoma famelica Casey 1916: 89. Type locality: "Lake Co., California" [**new synonymy**].

Type Material Studied. There is no specimen of *M. fulvipes* in Melsheimer's collection in the MCZ but the LeConte's collection includes six specimens under that name. The first one is labelled "(Pink disc)/ M. fulvipes Mels. opaca Ziegler [handwritten]" and the five others "Garland Col. 25.6". The first specimen agrees well with the original description and could be a specimen from Melsheimer's collection. The specimen belongs to *M. picipes*, whereas the other five specimens belong to *M. myrmecophila*.

The Motschulsky collection contains two specimens under the name of *M. fulvipennis*. Both specimens, glued on one plate, are males. They are labelled: "(small, round, green label)/ Monotoma fulvipennis Motsch Am. bor. [handwritten]/ Lectotypus Monotoma fulvipennis Motsch [partly handwritten]". The specimen located on the posterior end of the plate is here designated as the lectotype.

The Motschulsky collection contains two specimens under the name of *M. subnigra*. Both specimens, glued on one plate, are females. They are labelled: "(small, round, green label)/ Monotoma subnigrum Motsch Am. bor. [handwritten]/ Lectotypus Monotoma subnigra Motsch [partly handwritten]". The specimen on the anterior end of the plate is here selected as the lectotype.

Casey's collection in the USNM contains a single specimen under the name of *M. obsolescens* labelled "D.C./ Casey bequest 1925/ Type USNM 49188/ obsolescens Csy [handwritten]". The specimen, a female, is the holotype, since Casey (1916) specified having seen a single example.

Casey's collection in the USNM includes two specimens under the name of *M. famelica*. One, a male, is labelled "Lake Co. cal/ Casey bequest 1925/ Type USNM 49185/ famelica Csy [handwritten]" and the other, a female, "Or/ Casey bequest 1925/ famelica 2 Paratype USNM 49185". The male specimen is here designated as lectotype and the label "Lectotype Monotoma famelica Csy des. Y.Bousquet '88" has been attached to it.

Notes about Synonymy. The type specimens of *M. fulvipennis*, *M. subnigra*, *M. obsolescens*, and *M. famelica* agree in external structures with the specimens of *M. picipes* we have seen from Europe and North America.

No type specimen of *M. fulvipes* has been found although one specimen in the LeConte's collection could be an authentic Melsheimer's specimen (see "Type Material Studied" section). Melsheimer (1844) mentions in the original description "head ... with two longitudinal impressions between and near the eyes". This character state applies only to *M. picipes*. We believe the name *M. fulvipes* is best placed in synonymy with *M. picipes*.

In the original description of *M. opaca*, Ziegler (1845) indicates that the "head [is] with a somewhat dilated, longitudinal impression each side between the eyes". Such character state applies only to *M. picipes*. LeConte (1855: 305) had already synonymized *M. opaca* with *M. fulvipes*.

Monotoma parallelocollis Motschulsky, 1868 has been listed as a junior synonym of *M. fulvipes* Melsheimer following Reitter's comments (1877). We have been unable to borrow the type material

of Motschulsky's species from the Zoological Museum, Moscow State University, where it is presumably deposited. The original description is very short and does not include any pertinent character states. We believe it is best to consider *M. parallelocollis* as a valid species, until the type material becomes available for study.

Diagnosis. This species is easily recognized among the species treated by the presence of a pair of deep longitudinal impressions on the frons.

Description. **Colouration**. Head and pronotum piceous to black, elytra brown to dark reddish brown, occasionally blackish or yellowish, humeral calli slightly paler. **Pubescence**. Setae on dorsum of body elongate, narrow, most of those on pronotum and elytra suberect. **Punctation**. Frons and pronotum with deep, large punctures separated by less than half their diameter, more or less subcontiguous particularly on side of pronotum. Metasternum posteromedially and first visible abdominal sternite medially (at least on anterior half) with rather coarse punctures. **Head** (Fig. 3). Frons with 2 deep longitudinal impressions; median area, between impressions, slightly raised. Female without projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, angulate. Eyes proportionally large; temples short, length 0.3–0.4 times that of longitudinal diameter of eyes, slightly divergent posteriorly. **Thorax**. Pronotum (Fig. 3) slightly elongate, 1.1–1.2 times as long as wide, widest usually just before level of posterior angles; sides slightly rounded; lateral indentations rather coarse; anterior angle protruding, its extremity rounded; posterior angle distinct, marked by protuberance; disc without impressions on anterior half in most specimens (a few specimens seen with 2 shallow impressions). **Abdomen**. Male first visible abdominal sternite with slight, oval, median depression; last visible abdominal sternite simple. **Male genitalia** (6 specimens dissected) (Fig. 13). Ventral lamina more or less truncate medially; dorsal lamina rounded; tegmen with extremity more or less rounded.

Length of body: 1.9–2.5 mm.

Distribution. This species has been recorded from many countries around the world and is regarded as cosmopolitan by Nikitsky (1986). In North America, its occurs from the Atlantic to the Pacific coasts. We have seen specimens in the United States from Arizona, California, Colorado, Connecticut, District of Columbia, Florida, Illinois, Indiana, Kentucky, Louisiana, Maine, Massachusetts, Michigan, Minnesota, Montana, Nevada, New Hampshire, New Mexico, New York, Oklahoma, Pennsylvania, Tennessee, Texas, Vermont, Virginia, Washington, and Wisconsin. We have seen specimens from the following Canadian localities: **Newfoundland**: Portugal Cove, 19.VII., 1.IX.1981 (CNCI) 3. **Nova Scotia**. Halifax (MMUM) 1. **New Brunswick**: Moncton (MMUM) 7. Kouchibouguac Nat. Pk., 21.IX.1977, Campbell & Smetana (CNCI) 10. French Lake, 2.VI.28, W.J. Brown (CNCI) 1. Pointe-du-Chêne (MMUM) 1. **Québec**. Outremont, 21.VII.17, J. Ouellet (CNCI) 4. Montréal, 21.IV.19, 10.V.19, 19.V.19, 26.V.19, 8.VI.19, 8.VI.21, 20.VI.22, 3.X.28, J. Ouellet (ORUM) 11; idem, 17.VII.1974, 21.VII.1974, 6.VII.1976, 28.VI.1977, 16.VII.1981, E.J. Kiteley (CNCI) 5. Montebello (CUIC) 3; idem, 25.VI.37, 26.VI.37, 8.VII.37, 10.VII.37, 13.VII.37, 22.VII.37, 29.VII.37, 31.VII.37, J. Ouellet (ORUM) 14. Berthierville, 15.VI.38, J. Ouellet (ORUM) 1. La Trappe, 2.VII.43, 1.VI.44, 2.VI.44, 2.VII.44, 31.VII.44, 1.VIII.44, 3.VIII.44, 17.VII.45, J. Ouellet (ORUM) 9. Saint-Rémi, 28.IX., J. Ouellet (ORUM) 2. Mistassini, 9.VII.44, 30.VII.44, A. Robert (ORUM) 2. Louiseville, 1.VIII.1975, L. LeSage (ORUM) 1. Longueuil, 2.VI.34, J. Ouellet (ORUM) 1. Rigaud, 26.VI.39, A. Robert (ORUM) 1. Parc de la Gatineau, 15–22.IV.1987, J. Denis & J. Huber (CNCI) 1. **Ontario**. Ottawa-Kanata, 25.V.1979, A.& Z. Smetana (CNCI) 2. Prince Edward Co., VII.17, J.F. Brimley (CNCI) 1. Rondeau Prov. Pk., Lakeshore Road, 6.VI.1985, A. Davies & J.M. Campbell (CNCI) 1. Wheatley, 24.VI.65 (FSCA) 1. Tilbury, V.67, K. Stephan (FSCA) 1. **Manitoba**. Winnipeg, 24.VI.11, J.B. Wallis (CNCI) 1. Brandon, 27.V.1951, C.F. Barrett (CNCI) 1. **Alberta**. Calgary, 20.VIII.1981, 28.VIII.1981, B.F. & J.L. Carr (CNCI) 2. **British Columbia**. Vancouver Is. (MCZ) 1. Vancouver, Stanley Pk., IX.67, W. Lasorko (FSCA) 1. Victoria

(MCZ) 1. Lahache Lk. (MCZ) 1. Kaslo, 18.VII. (USNM) 1. Fort St. James, 1.VIII.95, S. Guthrie (CNC) 1.

Habitat. In decaying vegetable matter; also found under the bark of pine logs, in moss, seaweed and occasionally with ants (Peacock 1977).

Monotoma spinicollis Aubé, 1837
(Figs. 4, 14)

Monotoma spinicollis Aubé 1837: 463. Type locality: «environs de Compiègne [France]». Redtenbacher (1858: 378; 1874: 414); Wollaston (1867: 60; 1877: 41); Seidlitz (1872: 165; 1888: 240; 1889: 255); Reitter (1877: 5; 1901*a*: 194; 1901*b*: 4; 1911: 43); Fowler (1889: 255); Acloque (1896: 219); Everts (1899: 563; 1922: 252); Ganglbauer (1899: 576); Stierlin (1900: 566); Grouvelle (1908*a*: 21); Kuhnt (1912: 506); Hansen (1950: 147, 150); Hatch (1962: 251); Vogt (1967: 86); Kuschel (1979: 46); Ślipiński (1981: 9); Milander (1992: 70); Otero and Días-Pazos (1994: 103). *Monotoma spinifera* Wollaston 1857: 67. Type locality: «Ribiero de São Jorge», Madeira. Synonymy established by Wollaston (1864: 123)[1].

Type Material Studied. Aubé's collection in MHNP contains 7 specimens under the name *M. spinicollis*. Two of them, labelled "Corse" on the back of a mounting plate on which both are glued, are not syntypes. Of the remaining five specimens, the single male labelled "14 7^{bre} [= septembre ?] 1836 [handwritten on the back of the plate]/ Muséum Paris 1869 Coll. Ch. Aubé/ TYPE/ LECTOTYPE (♂) M. spinicollis Aubé Des. Bousquet & Laplante 1998" is designated as the lectotype. The male genitalia of the specimen were pulled out and mounted on a transparent plastic plate, in Canada balsam. The specimen is glued on a plate along with a female specimen.

We have seen one specimen of *M. spinifera* from the BMNH. The specimen, a male, is here designated as the lectotype. It is labelled: "Type/ spinifera, Woll. [handwritten]/ Lectotype M. spinifera Wollaston Des. Bousquet & Laplante 1998". The male genitalia of the specimen were pulled out and mounted on a transparent plastic plate, in Canada balsam.

Diagnosis. This species is recognized by features of the pronotum: the sides are distinctly and evenly rounded, the anterior angles are prominent, acute, usually oriented latero-anteriorly, and the posterior angles are indistinct.

Description. **Colouration**. Head and pronotum reddish brown to piceous, elytra usually paler, reddish yellow to reddish brown. **Pubescence**. Setae on dorsum of body elongate, wider than in *M. picipes*. **Punctation**. Frons and pronotum with large, deep, subcontiguous punctures. Metasternum posteromedially and first visible abdominal sternite medially (on anterior half) with coarse punctures. **Head** (Fig. 4). Frons without longitudinal impressions; median area slightly raised and somewhat depressed before posterior margin. Female without projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, clearly angulate. Eyes proportionally large; temples moderately long, length 0.5–0.6 times that of longitudinal diameter of eyes, very slightly divergent posteriorly. **Thorax**. Pronotum (Fig. 4) convex, slightly elongate, 1.1–1.2 times as long as wide, widest just behind middle; sides markedly rounded; lateral indentations coarse; anterior angle protruding, usually oriented latero-anteriorly, its extremity acute; posterior angle indistinct; disc without impressions on anterior half. **Abdomen**. Male first visible sternite

[1] Hetschko (1930: 99) listed "*spinigera* Chaud. Bull. Moscou XVIII, 1845, III, p. 211" as a junior synonym of *spinicollis* Aubé. We have found no reference to a *M. spinigera* in Chaudoir's paper of 1845. We believe the name does not exist.

without median depression; last visible sternite simple. **Male genitalia** (5 specimens dissected) (Fig. 14). Ventral lamina very narrowly emarginate medially; dorsal lamina rounded medially; tegmen shorter than median lobe, with extremity broadly emarginate.

Length of body: 2.0–2.6 mm.

Distribution. The species has been recorded from several countries in Europe and from New Zealand, eastern Africa, Cape of Good Hope (see Otero and Días-Pazos 1994), Asia Minor, Syria, Guadeloupe, Saint Vincent, and Grenada (see Blackwelder 1945). However, some of these records could be incorrect since there are two species confused under the name *M. spinicollis*. We have seen specimens of *M. spinicollis* from England, France, Dalmatia, Greece, Morocco, and from the United States (Massachusetts). We have seen a single specimen from Canada: **Ontario**. Ottawa, Mer Bleue, 16.IX.1980, R. Baranowski (CNCI) 1♂.

Habitat. In decaying vegetable matter (Peacock 1977).

Comments. In the course of this study, we found out that two species were included in the concept of *M. spinicollis*. The other species is described below under the name *M. johnsoni*.

Monotoma johnsoni Bousquet and Laplante, n.sp.

Etymology. Patronymic; named in honour of Colin Johnson who kindly provided specimens of this and other species for our study.

Type Material. Holotype (♂) labelled: "Kerrville, TEX. April 4 1959 Becker & Howden/ Holotype Monotoma johnsoni Bousquet & Laplante CNC No. 22422". The specimen is deposited in the Canadian National Collection of Insects.

Paratypes from the following localities. **United States of America**. *California*. Pasadena, April, Dr. A. Fenyes (CUIC, MCZ) 2♂,2♀. Anaheim, 7.VI.74 (FSCA) 1♂. *Oregon*. Philomath, 14.IV.1960, Harold Foster (USNM) 1♂. *Oklahoma*. Latimer Co., 1 mi E Panola, 3.VII.1987, D. Chandler & K. Stephan (NHDE) 3♂,1♀. *Hawaii*. Barbers Point, Oahu, 3.60 E.J. Ford Jr. (USNM) 1♂. **Brazil**. Nova Teutonia, Santa Catarina, F. Plaumann (MCZ) 1♂. **Portugal**. Algarve, Alvor, Portimão, 2-14.VIII.1992, C. Johnson (MMUM) 1♂. **Ethiopia**. Addis Abeba,, XII.73, G. de Rougemont (MMUM) 1♂. **Australia**. New South Wales, Cumberland, B.G. Rye (MMUM) 1♂.

Diagnosis. This species is very similar to *M. spinicollis* but differs by the character states listed below.

Description. Same character states as *M. spinicollis* except for the followings. **Head** (Fig. 24). Eyes slightly more protruding. **Thorax**. Pronotum (Fig. 24) with lateral sides usually less evenly rounded; anterior angle usually oriented more laterally; basal impressions slightly deeper. **Abdomen**. Male first visible abdominal sternite slightly convex, its punctuation usually slightly coarser. **Male genitalia** (9 specimens dissected). Aedeagus as in Fig. 23.

Distribution. The species is probably widely distributed in the world. We have seen specimens from the New World, Europe, Africa, and Australia. The species has not yet been found in Canada but is included in this work because of the possibility that it occurs there.

Habitat. The specimen from Ethiopia come from "compost heap". The specimen from Portugal was sieved from decaying vegetational rubbish (C. Johnson, pers. comm.).

Monotoma quadrifoveolata Aubé, 1837

Monotoma quadrifoveolata Aubé 1837: 468. Type locality: «environs de Compiègne [France]». Redtenbacher (1849: 203; 1858: 377; 1874: 414); Seidlitz (1872: 164; 1888: 240; 1889: 255); Reitter (1877: 4; 1884: 272; 1901*a*: 193; 1901*b*: 3; 1911: 42); Horn (1879: 260); Fauvel (1895: 108); Acloque (1896: 219); Everts (1899: 563; 1922: 251); Ganglbauer (1899: 574); Stierlin (1900:

566); Blatchley (1910: 668); Kuhnt (1912: 506); Hansen (1950: 146, 149); Vogt (1967: 84); Ślipiński (1981: 6); Nikitsky (1986: 1627).
Monotomina quadrifoveolata: Otero (1991: 255).

Recognition. This species is easily recognized by the two longitudinally confluent oval impressions on each side of the pronotum.

Description. **Colouration**. Body dorsally uniformly yellowish to reddish, sometimes reddish brown. **Pubescence**. Setae elongate, wider than in *M. picipes*. **Punctation**. Frons and pronotum scabrous, with rather small, deep punctures (which are mostly hidden by the setae). Metasternum posteromedially and first visible abdominal sternite medially (on anterior half) with coarse punctures. **Head** (Fig. 5). Frons without longitudinal impressions; median area slightly raised but sharply declivous posteriorly. Female without projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, angulate. Eyes proportionally small; temples long, length 1.2–1.5 times that of longitudinal diameter of eyes, more or less parallel. **Thorax**. Pronotum (Fig. 5) subquadrate to slightly elongate, 1.0–1.1 times as long as wide; sides parallel; lateral indentations small, sometimes more or less distinct; anterior angle not protruding, its extremity rounded; posterior angle distinct; disc with 4 deep impressions confluent into 2 longitudinal furrows. **Abdomen**. Male first visible sternite with slight, oval, median depression; last visible sternite simple. **Male genitalia** (3 specimens dissected) (Fig. 15). Ventral lamina notched medially; dorsal lamina narrowly truncate medially; tegmen with extremity rounded and crenulate.

Length of body: 1.9–2.3 mm.

Distribution. This species has been reported from many countries around the world and is regarded as cosmopolitan (Nikitsky 1986). In North America, we have seen specimens from Illinois, Minnesota, New Mexico, New York, Pennsylvania, Washington DC, and from the following Canadian locality: **Ontario**. Tilbury, Kent Co., V.1967, K. Stephan (CNCI) 4♂, 3♀.

Habitat. In decaying vegetable matter (Peacock 1977).

Comments. This species has been included within the subgenus *Gyrocecis* by several authors. We have found no character states that would suggest that *M. quadrifoveolata* is indeed closely related to the other species of *Gyrocecis*. Nikitsky (1986) created the subgenus *Monotomina* for *M. quadrifoveolata*.

Monotoma producta LeConte, 1855

Monotoma productum LeConte 1855: 305. Type locality: "New York".
Monotoma producta: Horn (1879: 259); Blatchley (1910: 668); Downie and Arnett (1996: 987).

Type Material Studied. LeConte's collection in the MCZ includes four specimens under the name *M. producta*. They are labelled as follows: specimen 1 "(Pink disc)/ Type 7040/ Monotoma productum Lec."; specimens 2 and 3 "(Pink disc)"; specimen 4 "O". The first specimen, a male, is here designated as the lectotype and the label "Lectotype Monotoma producta LeC. des. Y. Bousquet '87" has been attached to it.

Diagnosis. This species is easily recognized by features of the pronotum which is usually distinctly elongate, with the sides divergent posteriad, the anterior angles blunt, and the posterior angles marked by large protuberances.

Description. **Colouration**. Body dorsally uniformly reddish brown to piceous. **Pubescence**. Setae on dorsum rather short, narrow, more or less recumbent. **Punctation**. Frons and pronotum with large, deep, subcontiguous punctures. Metasternum posteromedially and first visible abdominal sternite medially with coarse punctures; visible abdominal sternites 2–4 each with row of large

punctures. **Head** (Fig. 6). Frons without longitudinal impressions; median area slightly raised. Female with small, median projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, rounded to slightly angulate. Eyes proportionally large; temples moderately long, about 0.6 times longitudinal diameter of eyes, parallel anteriorly, convergent posteriorly. **Thorax**. Pronotum (Fig. 6) usually elongate 1.1–1.3 times (most specimens seen 1.2 times or more) as long as wide, widest at level of posterior angles; sides divergent posteriorly; lateral indentations rather fine; anterior angle slightly protruding (usually less so than posterior angle), its extremity blunt; posterior angle distinct, marked by coarse protuberance; disc without impressions on anterior half. **Abdomen**. Male first visible abdominal sternite with oval, median depression; last visible abdominal sternite simple; female with apical margin of last visible sternite truncate and flanked by minute protuberances. **Male genitalia** (4 specimens dissected) (Fig. 16). Ventral lamina notched medially; dorsal lamina slightly truncate to rounded medially; tegmen with extremity rounded.

Length of body: 2.5–3.2 mm.

Distribution. This species occurs along the Atlantic Coast, from New Brunswick to Florida. We have seen specimens from the following states: Connecticut; Florida; Georgia; Maine; Maryland; Massachusetts; New Hampshire; New Jersey; New York; Virginia. One specimen seen from Reno Co., Kansas [FMNH] is likely mislabelled. In Canada, the species is known from one locality only: **New Brunswick**: Kouchibouguac Nat. Pk., 1.VI.1977, S.J. Miller (CNCI) 1♂, 1♀; idem, 2.VII.1977, J.R. Vockeroth (CNCI) 1♀.

Habitat. According to labels, this species has been collected in numbers by sifting wrack and looking under boards along beaches.

Monotoma myrmecophila Bousquet and Laplante, n.sp.

Etymology. From the Greek myrmec (ant) and phil (like), in reference to the fact that the species is found in ant nests.

Type Material. Holotype (♂) labelled: "Aweme, Man. 10.IX.28 R.M. White/ Holotype Monotoma myrmecophila Bousquet & Laplante CNC No. 22423". The specimen is deposited in the Canadian National Collection of Insects.

Paratypes from the following localities. **Canada**. *Manitoba*: Aweme, 30.V.27, R.M. White (CNCI) 1♂; idem, 10.IX.28 (CNCI) 1♂, 1♀. *Alberta*: Calgary, 27.V.57, Carr (CNCI) 1♂, 3♀; idem IV.1957, BF & JL Carr (USNM) 1♂. **United States of America**. *Colorado*: Garland, 25.VI. (MCZ, USNM) 8♂, 9♀. *Iowa*: Iowa City, Wickham (USNM) 1♂, 2♀. *Michigan*: Detroit (USNM) 1♂. *Nebraska*: West Point (USNM) 5♂, 4♀. *North Dakota*: Hebron 7.X.1928 (USNM) 2♀.

Diagnosis. This species is easily recognized by the short and wide setae on the dorsum of the body.

Description. **Colouration**. Head mostly dark reddish brown to piceous, pronotum reddish brown to rufopiceous, elytra often slightly paler than pronotum, reddish brown. **Pubescence**. Setae on dorsum of body short, wide, wedge-shaped, more or less recumbent. **Punctation**. Punctures slightly deeper than in other species treated. Frons and pronotum with large, subcontiguous punctures. Metasternum posteromedially and first visible abdominal sternite medially with large, subcontiguous punctures. **Head** (Fig. 7). Frons without longitudinal impressions; median area slightly raised. Female without projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, angulate. Eyes slightly less protruding than in *M. picipes*; temples moderately long, length 0.6–0.8 times that of longitudinal diameter of eyes, usually slightly divergent on basal half, then convergent. **Thorax**. Pronotum (Fig. 7) slightly elongate, 1.1–1.2 times as long as wide, widest at posterior angles; sides more or less parallel in anterior fourth,

widened and then slightly divergent in posterior half; lateral indentations rather coarse; anterior angle protruding, its extremity rounded; posterior angle more or less marked by large indentation, without protuberance; disc without foveae on anterior half. **Abdomen**. Male first visible abdominal sternite with slight, median, oval depression; last visible abdominal sternite simple. **Male genitalia** (3 specimens dissected) (Fig. 17). Ventral lamina deeply notched medially; dorsal lamina truncate medially; tegmen with extremity rounded.

Length of body: 2.0–2.7 mm.

Distribution. This species occurs from Michigan to Alberta, south to Colorado. It is known in Canada from two localities (see "Type Material" section).

Habitat. Apparently associated with ants. All ants collected with the specimens we saw belong to the genus *Formica* (*rufa* group).

Comments. Members of this species were identified in several collections as *M. fulvipes*. However, as mentioned previously (see section "Notes about Synonymy" of *M. picipes*), *M. fulvipes* is very likely a junior synonym of *M. picipes*.

This species belongs to the subgenus *Gyrocecis* Thomson, 1863 along with *M. angusticollis* Gyllenhal, 1827 and *M. conicicollis* Guérin-Méneville, 1829. These three species differ readily by their short, wedge-shaped setae on the dorsum of the body. All three species live in nests of *Formica* species.

Monotoma testacea Motschulsky, 1845

Monotoma testacea Motschulsky 1845: 97. Type locality: «bords du fleuve Irtych». Reitter (1901*a*: 196; 1901*b*: 6; 1911: 43); Kuhnt (1912: 507); Everts (1922: 253); Hansen (1950: 148, 149); Vogt (1967: 86); Peacock (1977: 13); Kuschel (1979: 45); Ślipiński (1981: 9); Hansen and Kristensen (1991: 44); Milander (1992: 71); Otero and Días-Pazos (1994: 101).
Monotoma quadraria Casey 1916: 90. Type locality: San Francisco, California [**new synonymy**].

Type Material Studied. Casey's collection in the USNM has a single specimen under the name *M. quadraria*. It is labelled: "Cal/ Casey bequest 1925/ type USNM 49187/ quadraria Casey". The label "Lectotype Monotoma quadraria Csy des. Y.Bousquet '87" has been attached to it.

Notes about Synonymy. We have compared the external characters and the male genitalia of several specimens of *M. quadraria* with eight specimens of *M. testacea* from England (determined by Colin Johnson) and found no structural differences.

Diagnosis. This species can be recognized by its rather uniform reddish colouration, by the shape of the pronotum with its sides slightly sinuate or parallel, and by the presence, in most specimens, of two very shallow impressions on anterior half of the disc.

Description. **Colouration**. Body more or less uniformly reddish dorsally or elytra slightly paler than forebody, somewhat reddish yellow. **Pubescence**. Setae on dorsum of body elongate, slightly wider than in *M. picipes*. **Punctation**. Frons and pronotum with large, deep, more or less subcontiguous punctures. Metasternum posteromedially and first visible abdominal sternite medially (on anterior half) with coarse punctures. **Head** (Fig. 8). Frons without longitudinal impressions; median area slightly raised, then slightly depressed before posterior margin. Female without protuberance on posterior margin dorsally. Lateral margin, between eye and antennal insertion, somewhat angulate. Eyes proportionally smaller than in *M. picipes*; temples moderately long, length 0.6–0.8 times that of longitudinal diameter of eyes, parallel to very slightly divergent posteriorly. **Thorax**. Pronotum (Fig. 8) slightly elongate, 1.1–1.2 times as long as wide; sides slightly sinuate or parallel; lateral indentations slightly finer than in *M. picipes*; anterior angle slightly protruding, its extremity rounded; posterior angle distinct, marked by protuberance; disc with 2 very shallow,

sometimes indistinct, impressions on anterior half. **Abdomen**. Male first visible abdominal sternite with slight, oval, median depression; last visible abdominal sternite simple. **Male genitalia** (4 specimens dissected) (Fig. 18). Ventral lamina notched medially; dorsal lamina truncate medially; tegmen with extremity rounded.

Length of body: 1.8–2.2 mm.

Distribution. This species has been recorded from various European countries, Caucasus, Turkestan, Siberia, and New Zealand. We have seen specimens from Arizona, California, Idaho, Illinois, Kansas, Maryland, Massachusetts, New Hampshire, New York, Oklahoma, Oregon, and Texas. In Canada, it is known from the following localities: **Quebec**: Montréal (MCZ) 1; idem, 8.V.19, J. Ouellet (ORUM) 1. La Trappe, 24.V.44, J. Ouellet (ORUM) 1. **Ontario**. Ottawa, Mer Bleue, 21.VI.73, Smetana & Davies (CNCI) 1; Ottawa-Kanata, 25.V.1979, A.& Z. Smetana (CNCI) 1. **Saskatchewan**: Truax (CNCI) 1. Thrasher, 1.XII.1953, D.B. Waddell (CNCI) 2. Radville, 1.VIII.1954, D.B. Waddell (CNCI) 4. Drinkwater, 26.XI.1953, D.B. Waddell (CNCI) 2. **Alberta**: New Dayton, 20.VII.1954, D.B. Waddell (CNCI) 1.

Habitat. Some specimens of this species were collected, as indicated by their label data, in mill feeds and oat bins. Peacock (1977) recorded it from decaying vegetable matter and in granaries.

Monotoma bicolor A. Villa and G.B. Villa, 1835

Monotoma bicolor A. Villa and G.B. Villa 1835: 49. Type locality not mentioned. Ganglbauer (1899: 573); Reitter (1911: 43); Kuhnt (1912: 507); Everts (1922: 253); Hansen (1950: 148, 149); Vogt (1967: 86); Peacock (1977: 13); Kuschel (1979: 45); Ślipiński (1981: 10); Hansen and Kristensen (1991: 44); Milander (1992: 71); Otero and Días-Pazos (1994: 101).
Monotoma parallelum LeConte 1855: 305. Type locality: "New York" [**new synonymy**].
Monotoma parallela: Horn (1879: 260); Blatchley (1910: 669); Hatch (1962: 252); Downie and Arnett (1996: 987).

Type Material Studied. LeConte's collection in the MCZ includes two specimens under the name *M. parallela*. The first specimen, a female, is labelled: "(Pink disc)/ Type 7041/ M. parallelum LeC. N.Y." and the second one, a male, "Mic". Since LeConte originally mentioned that he had only one specimen from New York, the first specimen is regarded as the holotype.

Notes about Synonymy. We have compared the external structures and the male genitalia of several specimens of *M. parallela* from North America with 14 specimens of *M. bicolor* from France (most of them identified by Colin Johnson). No structural differences were found and the two names are considered synonyms.

Diagnosis. We have found no particular character state that would differentiate this species from the other ones at first sight. It is best recognized by the character states listed in the key.

Description. **Colouration**. Head and pronotum reddish brown, rufopiceous, or piceous, elytra paler, usually yellowish to pale reddish brown. **Pubescence**. Setae on dorsum of body elongate, narrow. **Punctation**. Frons and pronotum with large, deep, more or less subcontiguous punctures. Metasternum posteromedially and first visible abdominal sternite medially (on anterior half) with rather coarse punctures. **Head** (Fig. 9). Frons without longitudinal impressions; median area slightly raised. Female without projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, angulate. Eyes proportionally large; temples moderately long, length 0.5–0.6 times that of longitudinal diameter of eyes, divergent posteriorly. Antennomere 2 subequal to antennomere 3. **Thorax**. Pronotum (Fig. 9) slightly elongate, 1.05–1.15 times as long as wide; sides slightly rounded, sometimes more or less parallel; lateral indentations often only slightly outlined; anterior angle protruding but often slightly so, its extremity rounded; posterior angle

distinct, marked by small protuberance; disc without impressions on anterior half. **Abdomen**. Male first visible abdominal sternite with slight, oval, median depression; last visible abdominal sternite simple. **Male genitalia** (7 specimens dissected) (Fig. 19). Ventral lamina deeply notched medially; dorsal lamina truncate medially; tegmen with extremity rounded.

Length of body: 1.9–2.5 mm.

Distribution. This species has been recorded from various countries in Europe, North Africa, Caucasus, Syria, Siberia, and New Zealand. We have seen specimens in the United States from Arkansas, Arizona, California, District of Columbia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maine, Massachusetts, Michigan, New Hampshire, New York, North Carolina, Ohio, Oklahoma, Oregon, Pennsylvania, Tennessee, Vermont, Wisconsin. In Canada, the species is known from the following localities: **New Brunswick**. Pointe-du-Chêne (MMUM) 1. **Québec**. Montréal, 3.VII. (MCZ) 1; idem, 19.V.19, 8.VI.21, 15.V.22, 20.VI.22, 23.VI.34, 20.IX., J. Ouellet (ORUM) 16; idem, 25.V.35, A. Robert (ORUM) 2; idem, 8.V.1971, 20.VI.1971, 19.V.1975, E.J. Kiteley (CNCI) 3. La Trappe, 12.VI.33, 6.V.44, 12.V.44, 26.V.45, 9.VI.45, 13.VI.45, 28.VI.45, 29.VI.45, 17.VII.45, 24.V.47, 30.VI.47, 28.V.48, 1.VI.48, J. Ouellet (ORUM) 17. Berthierville, 15.VI.38, J. Ouellet (ORUM) 1. Longueuil (CCCH) 1. **Ontario**. Ottawa-Kanata, 25.V.1979, A.& Z. Smetana (CNCI) 12. Prince Edward Co., 27.IV.55, Brimley (CNCI) 2. Vineland Station, 11.VII.37 (CNCI) 1. Tilbury, 26.V.1966 (FSCA) 1; idem, 27.VI.1966, V.1967, VIII.1967, X.1967, XI.1967, K. Stephan (FSCA) 8. **Saskatchewan**. Drinkwater, 26.XI.1953, D.B. Waddell (CNCI) 1. **British Columbia**. Vancouver, 15.IV.32, K. Graham (CNCI) 1. Salmon Arm, 4.V.32, H. Leech (CNCI) 1.

Habitat. Mainly in decaying vegetable matter (Peacock 1977). Some of the specimens studied were collected "under grass pile", in "barnyard litter" and by "sifting - barn".

Monotoma arida Casey, 1916

Monotoma arida Casey 1916: 89. Type locality: "probably Colorado".
Monotoma avara Blatchley 1928: 65. Type locality: Royal Palm Park, Florida [**new synonymy**].

Type Material Studied. Casey's collection in the USNM includes four specimens under the name *M. arida*. They are labelled as follows: specimen 1 "L/ Casey bequest 1925/ Type USNM 49186/ arida Csy."; specimen 2 "L/ Casey bequest 1925/ arida-2/ Paratype USNM 49186"; specimen 3 as for specimen 2 except "arida-3"; specimen 4 as for specimen 2 except "arida-4". The first three specimens belong to this species, the fourth one to *M. bicolor*. The first specimen is here designated as the lectotype and the label "Lectotype Monotoma arida Csy des. Y.Bousquet '87" has been attached to it.

Blatchley (1928) described his *M. avara* from two males. One of them was designated as the lectotype by Blatchley (1930: 49). The specimen, housed in PURC, is labelled: "3587 [handwritten]/ TYPE/ Royal Palm Park, Fla. WSB 4-5-27 [date handwritten]/ Monotoma avara sp.nov. [handwritten]".

Notes about Synonymy. We compared the external structures of the lectotype of *M. avara* with those of several specimens of *M. arida*. No differences were noted and the two names are listed in synonymy. The male of *M. arida* is quite distinctive by the presence of a large and deep depression on the last visible abdominal sternite. The lectotype of *M. avara* has the abdomen missing. However, Blatchley (1928: 65) originally mentioned in his description "last ventral of male with a very large, rounded median concavity".

Diagnosis. Males of this species are distinguished by the presence of a deep, granulate depression on the last visible abdominal sternite. Females are similar to those of *M. americana* and *M. emarginata* but differ mainly in having the pronotum slightly elongate, not subquadrate.

Description. **Colouration**. Body dorsally more or less uniformly reddish brown to piceous, humeral calli paler. **Pubescence**. Setae on dorsum elongate, slightly wider than in *M. picipes*. **Punctation**. Frons and pronotum with large, deep, subcontiguous punctures. Metasternum posteromedially and first visible abdominal sternite medially with coarse punctures. **Head** (Fig. 10). Frons without longitudinal impressions; median area slightly raised. Female without projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, angulate. Eyes proportionally slightly more protruding than in *M. picipes*; temples short, length about 0.3 times that of longitudinal diameter of eyes, slightly divergent posteriorly. **Thorax**. Pronotum (Fig. 10) slightly elongate, 1.10–1.15 times as long as wide, widest near level of posterior angles; sides slightly rounded; lateral indentations rather coarse; anterior angle slightly protruding, its extremity rounded; posterior angle distinct, marked by protuberance; disc without impressions on anterior half. **Abdomen**. Male first visible abdominal sternite with slight, oval, median depression; male last visible abdominal sternite with large, round, relatively deep, granulate depression; female with last visible sternite simple. **Male genitalia** (5 specimens dissected) (Fig. 20). Ventral lamina notched medially; dorsal lamina truncate medially; tegmen with extremity rounded.

Length of body: 1.8–2.2 mm.

Distribution. This species ranges over eastern North America from southern Ontario to Texas. The type locality, "probably Colorado", is suspect since the state is outside the known range of the species. We have seen specimens from the following states: Alabama, Arkansas, Florida, Georgia, Illinois, Indiana, Kansas, Kentucky, Louisiana, Missouri, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas. We know but a single specimen from Canada: **Ontario**. Rondeau Prov. Park, Harrison Trail, 30.V.1985, A. Smetana (CNCI) 1♂.

Habitat. Little is known about the habitat requirements of this species. Blatchley (1928: 66) collected two specimens "from beneath the dried remains of a mass of very foetid shrimp carrion". The single Canadian specimen was taken by sifting fallen leaves and other debris in a deciduous forest with intermixed pines (A. Smetana, pers. comm.).

Monotoma americana Aubé, 1837

Monotoma americana Aubé 1837: 461. Type locality: "États-Unis d'Amérique". Horn (1879: 260); Blatchley (1910: 668); Downie and Arnett (1996: 987).
Monotoma americanum: LeConte (1855: 305).
Monotoma corpulenta Motschulsky 1868: 200. Type locality: New Orleans, Louisiana [**new synonymy**].
Monotoma rhodeana Casey 1916: 91. Type locality: Boston Neck, Rhode Island [**new synonymy**]. Downie and Arnett (1996: 987).

Type Material Studied. Aubé's collection in MHNP contains one female specimen under the name *M. americana*, labelled: "Caroline du Sud. [handwritten]/ Muséum Paris 1869 Coll. Ch. Aubé/ TYPE". The specimen is the holotype, since Aubé originally mentioned he had a single specimen.

The Motschulsky collection contains two specimens under the name *M. corpulenta*. Both specimens are males, glued to the same plate. They are labelled: "[very small, square, orange label]/ [small, round, green label]/ Monotoma corpulentum Motsch Am. b. N.Orl [handwritten]/ Lectotypus Monotoma corpulenta Motsch [partly handwritten]." The posterior specimen has the genitalia extracted, and is here designated as the lectotype.

Casey's collection includes one female specimen under the name *M. rhodeana* labelled "R.I./ Casey bequest 1925/ Type USNM 49189/ rhodeana Csy [handwritten]". The specimen is here

designated as the lectotype and the label "Lectotype Monotoma rhodeana Csy. des. Y.Bousquet '88" has been attached to it.

Notes about Synonymy. The external structures and the male genitalia of the lectotype of *M. corpulenta* were compared with those of several specimens of *M. americana*. No important structural differences could be observed and the two names are considered synonyms.

The external structures of the lectotype of *M. rhodeana* and of several specimens of *M. americana* were compared. No differences were observed and both names are considered synonyms.

Diagnosis. We have observed no character state that would easily distinguish this species at first sight. It may be recognized by the character states given in the key.

Description. **Colouration**. Body dorsally more or less uniformly rufopiceous to piceous, humeral calli paler. **Pubescence**. Setae on dorsum elongate, narrow. **Punctation**. Frons and pronotum with large, deep, subcontiguous punctures. Metasternum posteromedially and first visible abdominal sternite medially with coarse punctures. **Head** (Fig. 11). Frons without longitudinal impressions; median area slightly raised. Female with small, hornlike, median projection on posterior margin dorsally. Lateral margin, between eye and antennal insertion, angulate. Eyes proportionally slightly more protruding than in *M. picipes*; temples short, length about 0.3 times that of longitudinal diameter of eyes, usually slightly divergent posteriorly. **Thorax**. Pronotum (Fig. 11) convex, subquadrate, 1.00–1.07 times as long as wide, widest near level of posterior angles; sides straight to slightly rounded; lateral indentations rather coarse; anterior angle slightly protruding, its extremity rounded; posterior angle distinct, marked by protuberance; disc without impressions on anterior half. **Abdomen**. Male first visible abdominal sternite with slight, oval, median depression; male last sternite with more or less round, shallow (sometimes almost indistinct) depression; female with last visible sternite simple. **Male genitalia** (61 specimens dissected) (Fig. 21). Ventral lamina notched medially; dorsal lamina truncate medially; tegmen with extremity slightly emarginate.

Length of body: 1.9–2.4 mm.

Distribution. This species is widely distributed over the United States from coast to coast. We have seen it from three localities in Canada: **Québec**. La Trappe, 25.VI.44, 20.VI.47, J. Ouellet (ORUM) 2♀. **Ontario**. Rondeau Prov. Pk., Lakeshore Road, 30.V.1985, A. Smetana (CNCI) 23♂, 14♀; idem, 1–6.VI.1985, A. Davies & J.M. Campbell (CNCI) 3♂, 10♀. Tilbury, V.1967, K. Stephan (FSCA) 2♀.

Habitat. Mainly in decaying vegetable matter, such as compost, grass clippings, and hay litter. The numerous specimens from Rondeau Provincial Park were collected in "sifted grass pile & leaves".

Comments. We observed variation in the shape of the tegmen of the male genitalia. Some specimens, particularly from southern United States, have the tegmen more deeply emarginate medially, though not as much as that of *M. emarginata*. Considering the wide distribution of the taxon in the United States, it could represent a complex of species.

Monotoma emarginata Bousquet and Laplante, n.sp.

Etymology. From the Latin emarginatus, -a, -um (notched at the apex), in reference to the deeply notched tegmen.

Type Material. Holotype (♂) labelled: "Ont. Ottawa-Kanata 25.V.1979 A&Z Smetana/ Holotype Monotoma emarginata Bousquet & Laplante CNC No. 22424". The specimen is deposited in the Canadian National Collection of Insects.

Paratypes from the following localities. **Canada**. *Ontario*: Ottawa-Kanata, 25.V.1979, A.& Z. Smetana (CNCI) 1♂, 2♀. **United States of America**. *Florida*: Tallahassee, Leon Co., 22.VI.1987, P. Skelley (FSCA) 1♂, 4♀. Ocala, Marion Co., 20.VII.19777, M.C. Thomas (FSCA) 1♂. Crescent City (USNM) 1♂. *Illinois*: Pine Hills Field Sta., Union Co., 15–22.V.1967, J.M. Campbell (CNCI) 1♂. *Indiana*: Indianapolis, 5.V.1965, C.E. White (FSCA) 1♂. *Kansas*. Lawrence, Douglas Co., 30.V.83, J. Pakaluk (USNM) 1♂. 2 mi. N Baldwin, Douglas Co., 16–24.V.1984, J. Pakaluk (USNM) 1♂. *Louisiana*: Baton Rouge, LSU Campus, 30.VI.1985, D.A. Rider (LSUC) 1♂, 1♀. *Missouri*. 1 mi. E Moberly, Randolph Co., 23.IV.73, E.G. Riley (TAMU) 1♂. 5 mi. NE Lawson, Ray Co., 4.VI.1972, E.G. Riley (TAMU) 1♂. *North Carolina*. Reidsville, Rockingham Co., 30.V.1973, J.S. Ashe (TAMU) 1♂, 1♀. *Oklahoma*: Latimer Co., various dates, K. Stephan (CNCI, FSCA) 9♂, 15♀. 5 mi. W Red Oak, Latimer Co., 9.IV.85, J. Pakaluk (USNM) 2♂; idem, XI.1978, X.1980, K. Stephan (FSCA) 2♀. *Texas*. Katy, II.1971, K. Stephan (FSCA) 1♀. *Wisconsin*: Kenosha, Kenosha Co., 12.XI.1962, W. Suter (FMNH) 1♂.

Diagnosis. This species is structurally very similar to *M. americana* but differs notably by the more deeply notched tegmen in the male and by the absence of a minute projection on the posterior margin of the head in the female.

Description. Same character states as *M. americana* except for the followings. **Head**. Posterior margin of female without projection medially. **Abdomen**. Last visible abdominal sternite of female with small longitudinal carina-like tubercle before apex in most specimens. **Male genitalia** (18 specimens dissected) (Fig. 22). Tegmen deeply notched at middle.

Distribution. This species lives in eastern North America from Ontario south to Florida and Texas. It is known in Canada from one locality (see "Type Material" section).

Habitat. The holotype and the paratypes from Ottawa-Kanata were taken by sifting a pile of moldy grass clippings (A. Smetana, pers. comm.). Numerous specimens from Latimer Co., Oklahoma, were collected from "oak tree hole".

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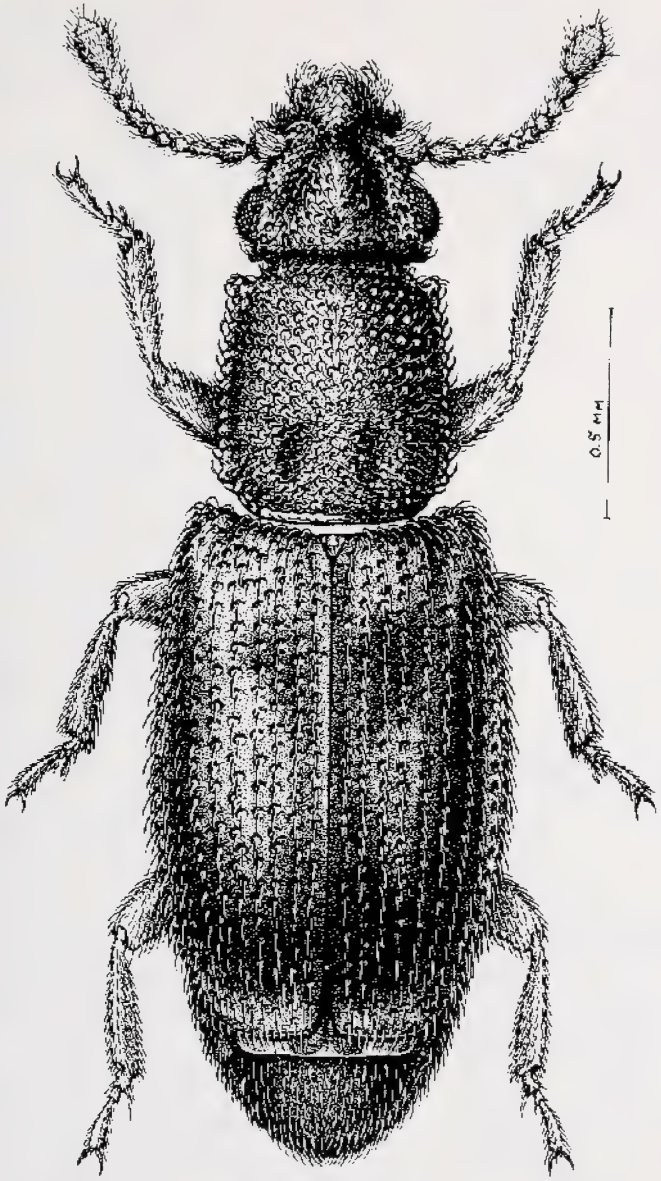
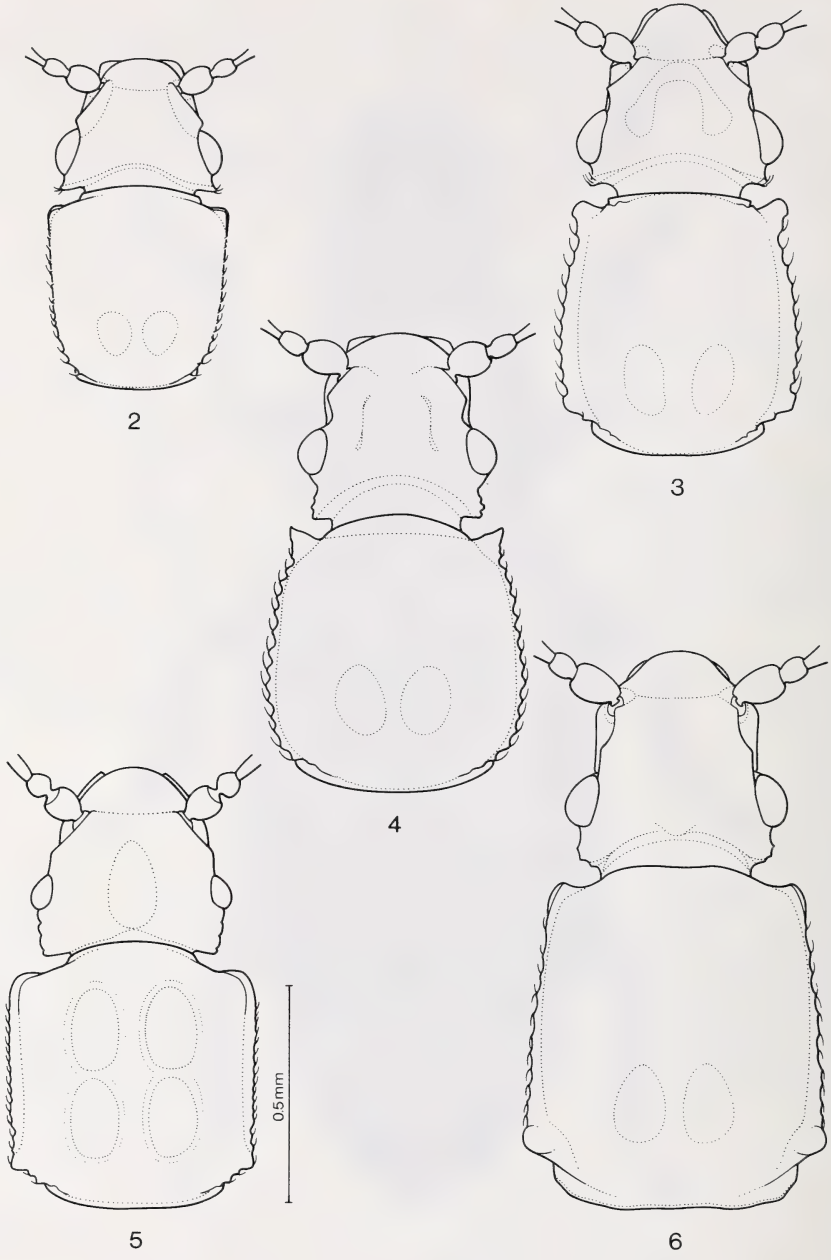
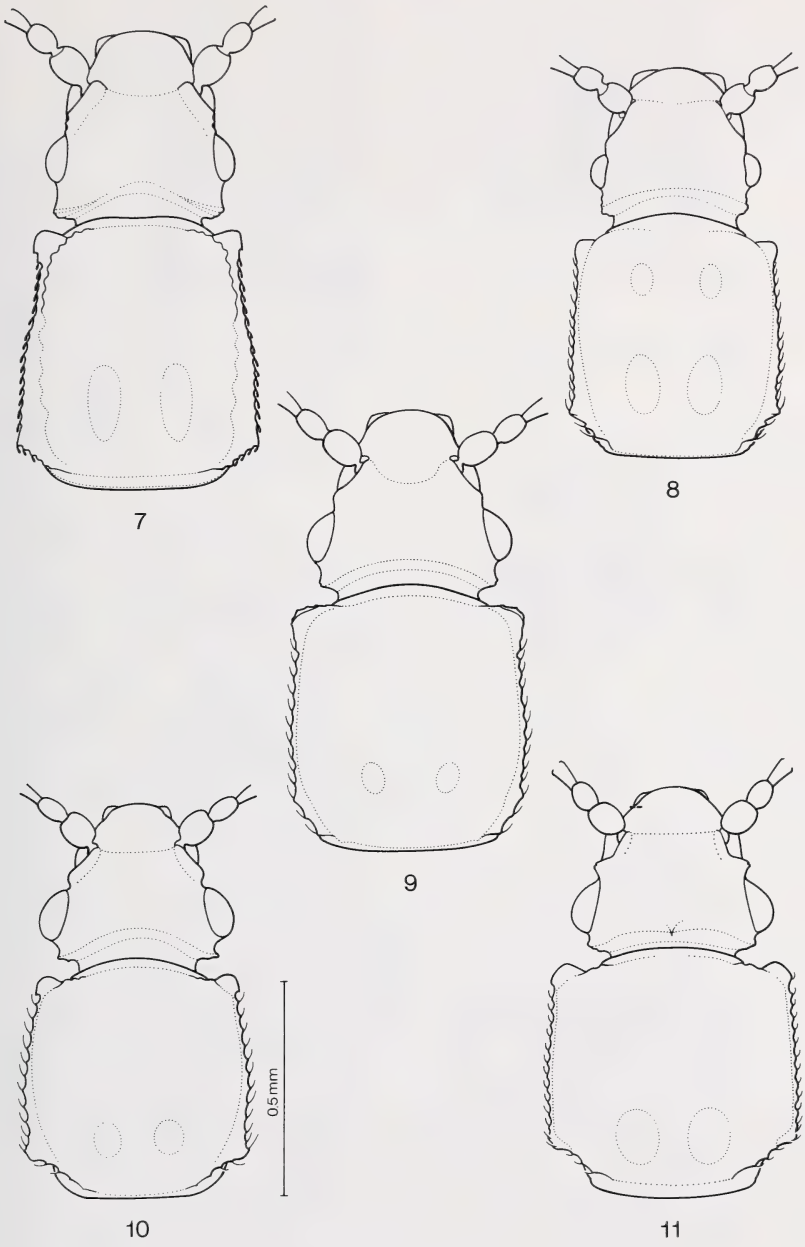


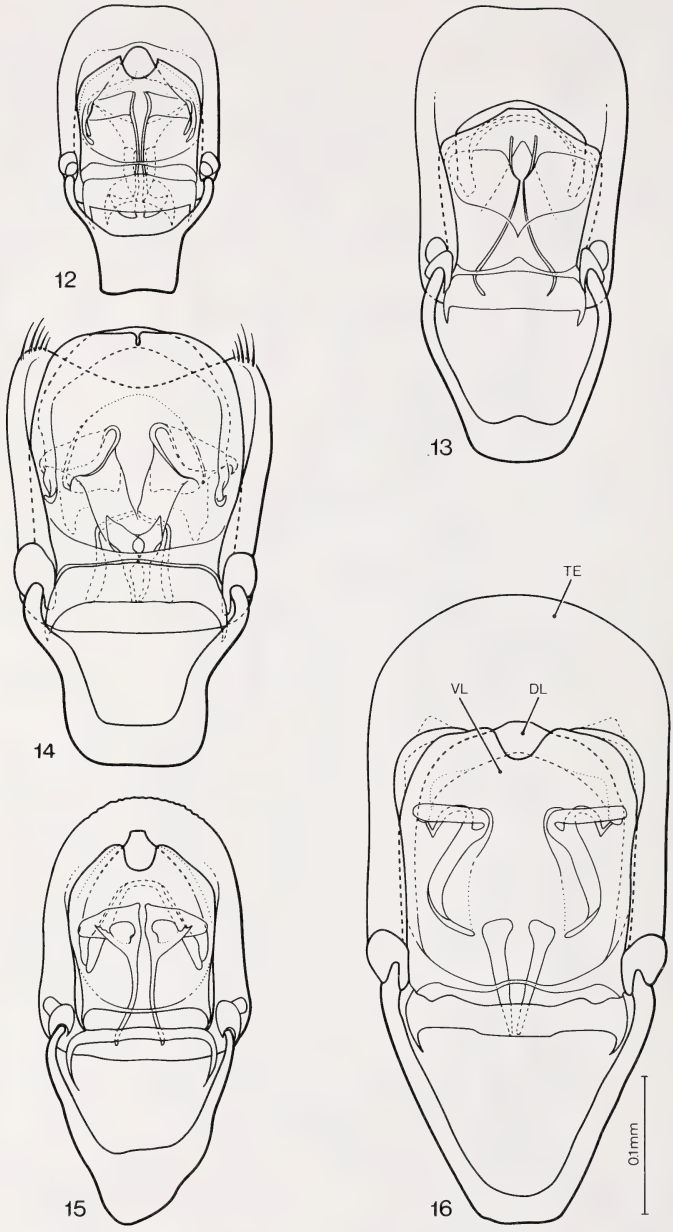
FIGURE 1. *Monotoma picipes* Herbst.



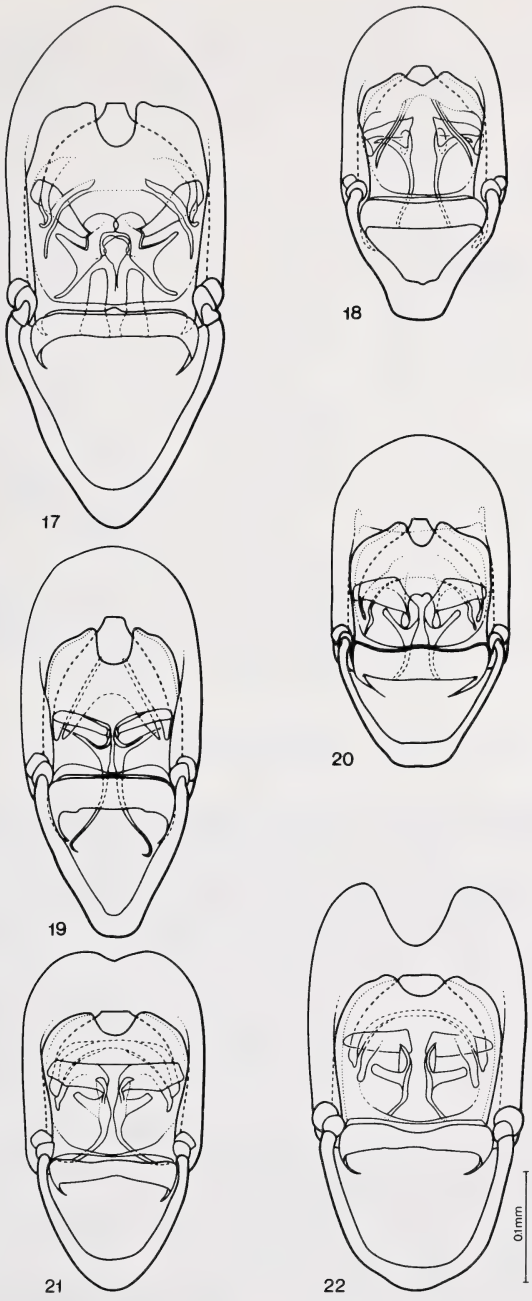
FIGURES 2–6. Head and pronotum. 2: *Monotoma longicollis*; 3: *M. picipes*; 4: *M. spinicollis*; 5: *M. quadrifoveolata*; 6: *M. producta*.



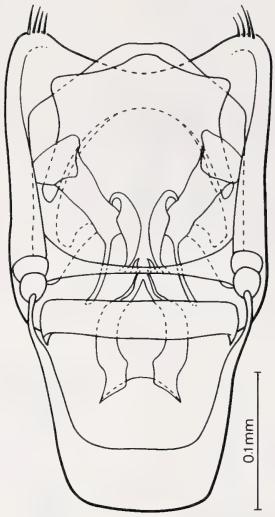
FIGURES 7–11. Head and pronotum. 7: *Monotoma myrmecophila*; 8: *M. testacea*; 9: *M. bicolor*; 10: *M. arida*; 11: *M. americana*.



FIGURES 12–16. Aedeagus (ventral view). 12: *Monotoma longicollis*; 13: *M. picipes*; 14: *M. spinicollis*; 15: *M. quadrifoveolata*; 16: *M. producta*. dl – dorsal lamina; te – tegmen; vl – ventral lamina.



FIGURES 17–22. Aedeagus (ventral view). 17: *Monotoma myrmecophila*; 18: *M. testacea*; 19: *M. bicolor*; 20: *M. arida*; 21: *M. americana*; 22: *M. emarginata*.



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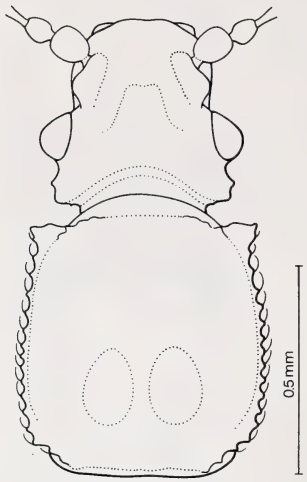

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FIGURES 23–24. *Monotoma johnsoni*. 23: aedeagus (ventral view); 24: head and pronotum.

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EICOSANOIDS MEDIATE NODULATION REACTIONS TO BACTERIAL INFECTIONS IN ADULTS OF THE AMERICAN COCKROACH, *PERIPLANETA AMERICANA* (L.)

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Abstract *Proc. ent. Soc. Ont.* 130: 97–108

Nodulation is the first, and qualitatively predominant, cellular defense reaction to bacterial infections in insects. We tested the hypothesis that eicosanoids mediate nodulation reactions to bacterial infections in adults of the American cockroach, *Periplaneta americana*. Treating experimental cockroaches with the eicosanoid biosynthesis inhibitor, dexamethasone, strongly impaired nodulation reactions to bacterial infections. The influence of dexamethasone was reversed by treating infected insects with arachidonic acid, an eicosanoid precursor. Several other eicosanoid biosynthesis inhibitors, including the lipoxygenase inhibitor, esculetin, and the cyclooxygenase inhibitors ibuprofen and naproxen, also impaired the ability of experimental cockroaches to form nodules in reaction to bacterial infections. The influence of two inhibitors, phenidone and esculetin, were expressed in a dose-dependent manner. These findings support the hypothesis that eicosanoids mediate cellular immune responses to bacterial infections in cockroaches, and more broadly, in insects.

Introduction

Hemocytic immune reactions to bacterial infections involve direct cellular interactions between circulating hemocytes and bacteria. Specific cellular defense mechanisms include phagocytosis, nodulation and encapsulation (Gupta 1986, 1991). While humoral and hemocytic immune reactions to bacterial infections are well documented, until recently there was virtually no information on the biochemical events responsible for mediating insect immune reactions. Drawing on the background of signal transduction systems in mammalian immunity, Stanley-Samuelson et al. (1991) suggested insect cellular immune reactions are mediated by eicosanoids. Eicosanoids are oxygenated metabolites of arachidonic acid and two other polyunsaturated fatty acids (Fig. 1). There are three major groups of eicosanoids. One includes the prostaglandins, another the epoxyeicosatrienoic acids. The third group is composed of the many lipoxygenase products. Eicosanoids are very well understood in the contexts of human and animal medicine, where they mediate many pathophysiological events, such as inflammation. Eicosanoids also are important for many actions in invertebrates, all detailed in recent reviews (Stanley-Samuelson 1994a,b; Stanley and Howard 1998; Stanley 1999).

In our initial investigations we determined that treating tobacco hornworms, *Manduca sexta*, with pharmaceutical inhibitors of eicosanoid biosynthesis rendered experimental hornworms unable to clear bacterial infections from hemolymph circulation. We inferred from these observations that

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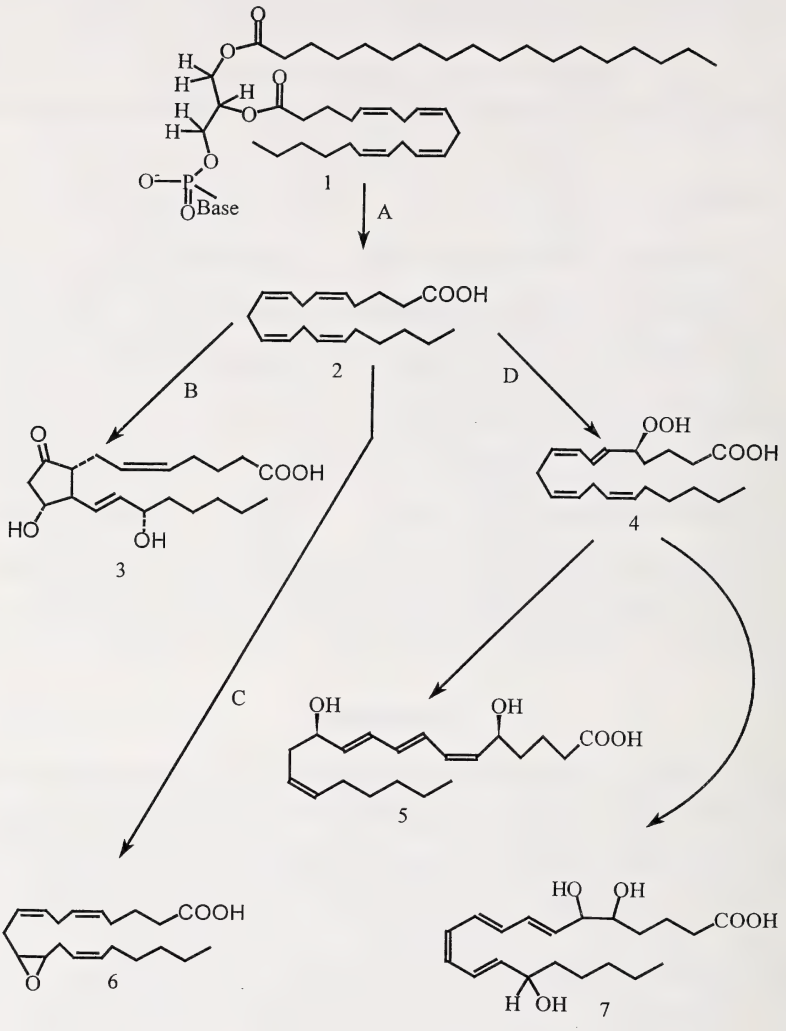

FIGURE 1. An overview of 20:4n-6 metabolism as understood from mammalian physiology. Three polyunsaturated fatty acids, 20:3n-6, 20:4n-6 and 20:5n-3 are potential substrates for eicosanoid biosynthesis. Of these, metabolism of 20:4n-6 is most well studied. Chemical structures are denoted by numerals. **1** = a cellular phospholipid. **2** = hydrolyzed 20:4n-6. **3** = prostaglandin E_2. **4** = 5-hydroperoxyeicosatetraenoic acid. **5** = leukotriene B_4. **6** = 11,12-epoxyeicosatrienoic acid. **7** = lipoxin A. Capital letters indicate major enzyme systems responsible for eicosanoid biosynthesis. **A** = phospholipase A_2; **B** = cyclooxygenase and associated enzyme steps; **C** = cytochrome P_{450} epoxygenase; **D** = lipoxygenase.

some or all of the cellular defense reactions responsible for clearing bacterial infections from hemolymph are mediated by eicosanoids (Stanley-Samuelson et al. 1991). This was the first suggestion of a signal transduction system in invertebrate cellular immunity.

This work prompted more detailed experiments designed to determine which of the several cellular defense reactions depend on eicosanoid biosynthesis. Nodulation is an early insect cellular defense reaction responsible for clearing large numbers of bacterial cells from circulation during the first two hours of an infection (Horohov and Dunn 1983). Because nodulation is the predominant cellular reaction to bacterial infections, we hypothesized that eicosanoids mediate nodulation reactions to bacterial infections. We tested this idea by injecting hornworms with an eicosanoid biosynthesis inhibitor, then infecting them with bacteria. Compared to ethanol-treated controls, the experimental larvae produced far fewer nodules in response to similar bacterial challenges. We also showed that the influence of the eicosanoid biosynthesis inhibitor, dexamethasone, could be reversed by treating the experimental larvae with arachidonic acid, the immediate precursor of eicosanoids. We concluded that nodulation is one of the cellular immune responses to bacterial infections that is mediated by eicosanoids (Miller et al. 1994).

On the basis of these findings on a single lepidopteran species, we developed the hypothesis that eicosanoids mediate nodulation reactions to bacterial infections in most, if not all, insect species, now known as the eicosanoid hypothesis (Stanley and Howard 1998; Stanley 1999). Using similar experimental protocols, we have shown that nodulation reactions to bacterial infections depend on eicosanoid biosynthesis in the tenebrionid beetle, *Zophobas atratus* (Miller et al. 1996), in the silkworm, *Bombyx mori* (Stanley-Samuelson et al. 1997) and in two other moths, black cutworms, *Agrotis ipsilon* and true armyworms, *Pseudaletia unipuncta* (Jurenka et al. 1997). In related work, Mandato et al. (1997) found that cell spreading and prophenyloxidase activation, two distinct phases of nodulation, and phagocytosis are mediated by eicosanoids in waxmoths, *Galleria mellonella*. These findings support the eicosanoid hypothesis to the extent that several lepidopteran species represent the Class Insecta.

To consider a broader phylogenetic range of insect species, Miller et al. (1999) investigated the hypothesis in adults of a hemimetabolous insect, the cricket *Gryllus assimilis*. Similarly, Tunaz et al. (1999) conducted a parallel series of experiments with two species of 17-year periodical cicadas, *Magicicada septendecim* and *M. cassini*. Again, all experimental results support the hypothesis. On the basis of these findings, we suggested that eicosanoids mediate cellular immune reactions in hemimetabolous insects (Miller et al. 1999). However, this broader hypothesis is weakened because the eicosanoid hypothesis has been tested in only three hemimetabolous insect species. To address this shortcoming, we tested the hypothesis in adults of the American cockroach, *Periplaneta americana*, a hemimetabolous insect species representing the Orthopteroidea. Here we report that adults of this species form nodules in response to bacterial infections, and that the nodulation response is impaired by treating the cockroaches with eicosanoid biosynthesis inhibitors just prior to infection. In view of the widespread use of this species in insect immunity, these results facilitate future work on insect immunity.

Materials and Methods

Organisms

A culture of cockroaches, *P. americana*, was provided by Johnson and Johnson, Inc. All stages of the insects were maintained in a 50-gallon container partitioned with egg-crates and provisioned with dog chow and water. The containers were kept on laboratory benches at room temperature and exposed to a natural photoperiod. Male and female cockroaches were randomly used in all experiments.

Cultures of a non-pigmented strain of the bacterium *Serratia marcescens* and nutrient broth (Difco) were purchased from Carolina Biological Supply (Burlington, NC). Bacteria were grown in 50 ml of nutrient broth in an environmental shaker at 37°C and 100 rpm. Bacteria were grown to a titre of (10^7) colony forming units/ml, and used in stationary phase.

Injections and assays for nodulation

We followed the protocols formalized by Miller and Stanley (1998). Before injections, cockroaches were surface sterilized by swabbing their cuticle with 95% ethanol. We injected adult cockroaches with either the phospholipase A_2 (PLA_2) inhibitor dexamethasone {(11ß, 16)-9-fluoro-11,17,21-trihydroxy-16-methylpregna-1,4-dione}, one of the cyclooxygenase inhibitors, ibuprofen {α -methyl-4 (2-methylpropyl) benzeneacetic acid}, indomethacin {1-P-(chlorobenzyl)-5-methoxy-2-methyl-3-indolyl-acetic acid}, naproxen {O-2-(6-methoxy-naphthyl) propionic acid}, or piroxicam {3,4-benzothiazine-3-carboxamide 1,1-dioxide}, the dual cyclooxygenase and lipoxygenase inhibitor phenidone {1-pheny-3-pryazolidinone}, or the 5- and 12-lipoxygenase inhibitor, esculetin {6,7-dihydroxycoumarin} (all inhibitors purchased from BioMol, Plymouth Meeting, PA). In rescue experiments, adults were injected also with arachidonic acid {5,8,11,14-eicosatetraenoic acid}, purchased from Sigma Chemical Co. (St. Louis, MO). Control insects were injected with 95% ethanol. Drugs and control substances were injected into the opposite side of the abdomen using a 10 µl Hamilton 701 syringe. All injections of pharmaceuticals were in a standard dosage of 26 µg in 3 µl of ethanol, except in dose-response experiments. The fatty acids were injected at dosages of 50 µg in 5 µl per adult cockroach.

Immediately after the drug injections, adult cockroaches were infected by injecting a standard bacterial dosage of 10^5 colony forming units/cockroach (Miller et al. 1994, 1996). Bacteria were injected in 10 µl aliquots, using a 26 gauge 0.5" needle attached to a 50 µl syringe (Hamilton, Reno, NV).

We assessed nodulation at selected times post infection (PI). We anesthetized cockroaches by chilling them on ice, then exposed their hemocoels. Melanized, brown nodules were counted under a stereo microscope at 60X. The nodules were distinct, and direct counting reliably reflected the extent on the nodulation response to infections (Miller et al. 1994, 1996; Miller and Stanley 1998). After the first counting, the alimentary canal was removed. Nodules in the previously unexposed areas and remaining internal tissues were then counted.

Control Experiments

To determine the level of the background nodulation in our cockroach colonies, we conducted several control experiments. To record the nodulation in unchallenged adults, 4 cockroaches were taken from culture at various times in this project. We anesthetized cockroaches on ice for 10 minutes, then assessed nodulation. To determine the influence of injection wounds on nodule formation, 4 adults were injected with a standard volume of ethanol, the drug vehicle. Nodulation was assessed 10 h later, following the same protocol. To assess the effect of dexamethasone on nodulation in unchallenged cockroaches, a standard dosage of dexamethasone in 3 µl ethanol was injected into 4 cockroaches. Nodulation was assessed by standard methods 10 h later. Finally, we tested the possibility that nutrient broth could stimulate nodulation by injecting 10 µl of broth into 4 cockroaches. Nodulation was assessed by standard methods 10 h later.

Time course of nodulation: Influence of dexamethasone

Individuals in two groups of cockroaches were injected with 10 µl of ethanol or with 26 µg of dexamethasone in 3 µl of ethanol. The cockroaches were immediately injected with bacteria as

described. At 2, 4, 8, 10, 12, 16 and 24 hours PI, sub-groups of control and experimental insects were anesthetized, and nodulation was assessed.

Dose-response curves for phenidone and esculetin

Individuals in six groups of cockroaches were injected with 10 µl of ethanol, or 0.0026, 0.026, 0.26, 2.6, 26 µg of phenidone in 3 µl ethanol, then infected with a standard dosage of bacteria. At 10 h PI, the cockroaches were anesthetized, and nodulation was assessed.

We used another drug, esculetin, to determine a dose-response curve for a specific lipoxygenase inhibitor, which has not been carried out for any invertebrate. Individuals in 3 groups of cockroaches were injected with 10 µl ethanol, or with 0.026 and 26 µg of esculetin in 3 µl of ethanol, then injected with a standard dosage of bacteria. After 10 h PI, the cockroaches were anesthetized, and nodulation was assessed.

Fatty acid rescue experiment

Individuals in two groups of adult cockroaches were injected with either 10 µl ethanol or 26 µg of dexamethasone in 3 µl of ethanol and then infected with bacteria as described. Immediately after infection, the dexamethasone-treated cockroaches were divided into two sub-groups. Individuals in one sub-group were treated with 50 µg arachidonic acid in 2 µl of ethanol. Another sub-group was treated with 5 µl of ethanol to control for the effects of the extra injection on nodulation. At 10 h PI, cockroaches were anesthetized and nodulation assessed.

Influence of other eicosanoid biosynthesis inhibitors on nodulation

We divided cockroaches into groups and injected individuals in each group with either one of the cyclooxygenase inhibitors indomethacin, naproxen, ibuprofen or piroxicam, the dual cyclooxygenase and lipoxygenase inhibitor phenidone, or the lipoxygenase inhibitor esculetin, all in standard dosages of 26 µg in 3 µl of ethanol. Control insects were injected with 10 µl of ethanol. Following injections, the cockroaches were infected with a standard dosage of bacteria as described. At 10 h PI, the cockroaches were anesthetized and nodulation was assessed.

Results

Control experiments

Table I displays the results of control experiments. We recorded approximately 5 nodules/cockroach (n=4 cockroaches) in untreated insects taken directly from the culture. Similarly, we observed approximately 5 nodules/insect in cockroaches injected with ethanol, and in cockroaches injected with dexamethasone. Injections with nutrient broth resulted in approximately 7 nodules/insect. By comparison, challenges with standard dosages of *S. marcescens* resulted in approximately 45 nodules per adult.

Time course of nodulation

The time course of visible nodule formation in two groups cockroaches, experimentals and controls, is shown in Figure 2. Dexamethasone-treated adults formed approximately 10 nodules/insect at 2 h PI, which increased to 23 at 10 h PI, whereas the ethanol-treated control adults produced significantly more nodules at each time, from 15 nodules at 2 h PI to 63 at 10 h PI (LSD, $p<0.001$). The numbers of nodules did not increase in cockroaches incubated longer than 10 h PI, and in all subsequent experiments nodulation was assessed at 10 h PI.

TABLE I. Outcomes of background control experiments. Cockroaches, *Periplaneta americana*, were treated as specified in the left column, and nodulation was assessed at 10 hours post-treatment as described in Materials and Methods.

Treatment	Nodules per adult (Mean ± SEM)
None	4.7 ± 1.4
Inject drug vehicle	7.0 ± 2.5
Inject dexamethasone	5.2 ± 2.7
Inject nutrient broth	7.0 ± 2.3
Inject bacteria in broth	48.2 ± 4.6

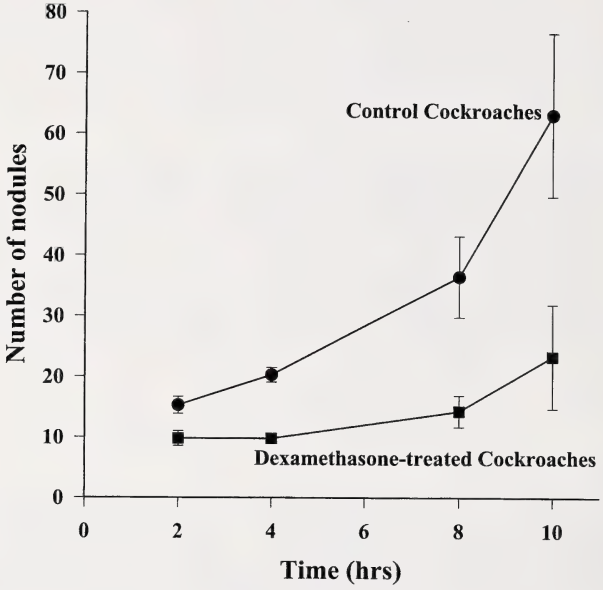

FIGURE 2. Time course of nodulation in adult cockroaches, *Periplaneta americana*, in response to intrahemocoelic infections with the pathogenic bacterium, *Serratia marcescens*. Each point indicates the mean number of nodules found in each insect (n=6 individuals), and the error bars represent 1 SEM.

Dose-response curves for phenidone and esculetin

The influence of phenidone and esculetin on nodulation in response to bacterial infections was expressed in a dose-dependent manner. Nodulation declined from approximately 46 nodules/ cockroach in ethanol-treated control cockroaches, to approximately 13 nodules/cockroach in cockroaches treated with the highest phenidone dosage (Fig. 3) and to approximately 10 nodules/

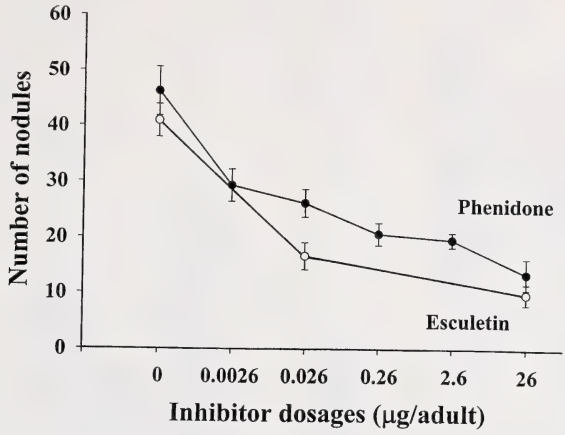

FIGURE 3. Dose-response curves for the influence of phenidone and esculetin on nodule formation in adults of *Periplaneta americana.* Each point indicates the mean number of nodules found in each insect (n=6 individuals) and the error bars represent 1 SEM.

cockroach in cockroaches treated with highest esculetin dosage (Fig. 3). For both pharmaceuticals, intermediate dosages produced intermediate nodulation reactions, approximately 15 to 30 nodules/ cockroach.

Influence of other eicosanoid biosynthesis inhibitors on nodulation

We considered the influence of seven pharmaceutical inhibitors of eicosanoid biosynthesis on nodulation in response to bacterial infections. As can be seen in Figure 4, compared to control (EtOH) cockroaches, all experimental cockroaches exhibited significantly reduced nodulation in response to bacterial infections (LSD, $p<0.001$). We did not obtain significant differences among the effects of individual inhibitors on nodulation.

Fatty acid rescue experiment

According to the evidence taken from research in mammalian physiology, dexamethasone, as one of its actions, inhibits eicosanoid biosynthesis through its effect on PLA_2 (Fig. 1). If this is true, then injecting the eicosanoid-precursor polyunsaturated fatty acid, arachidonic acid, into dexamethasone-treated infected adults should reverse the effects of dexamethasone on nodulation. To test this idea, we proceeded as follows: after injection with dexamethasone, adults were infected with bacteria and then immediately treated with arachidonic acid. To control for the influence of the third injection on nodulation, an additional control group of cockroaches was injected with ethanol. As can be seen in Figure 5, arachidonic acid treatments reversed the effects of dexamethasone on nodulation ($p<0.05$). The ethanol-injected control cockroaches yielded approximately 48 nodules/cockroach and dexamethasone-treated cockroaches approximately 17 nodules/ cockroach, both in line with expectation. The arachidonic acid-treated cockroaches produced approximately 70 nodules per cockroach, also in line with expectation for control animals. The second control group, injected with a second dose of ethanol, yielded approximately 14 nodules/ cockroach.

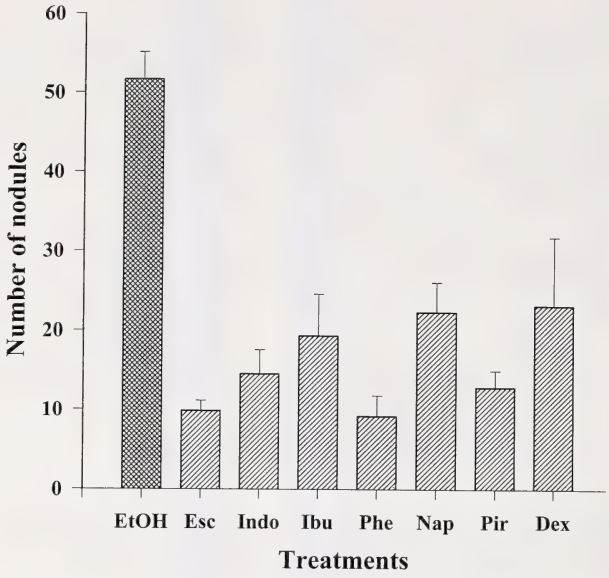

FIGURE 4. Effect of treating *Periplaneta americana* adults with individual eicosanoid biosynthesis inhibitors on nodule formation in response to intrahemocoelic infections with the insect pathogen, *Serratia marcescens*. Test insects were first injected with 26 µg of either dexamethasone (Dex; PLA_2 inhibitor), esculetin (Esc; lipoxygenase inhibitor), indomethacin (Indo), ibuprofen (Ibu), naproxen (Nap), or piroxicam (Pir), all cyclooxygenase inhibitors, phenidone (Phe; dual cyclooxygenase/lipoxygenase inhibitor). Control insects were first injected with ethanol (EtOH). The height of the histogram bars represents the mean number of nodules found in each insect (n=6 individuals) and the error bars represent 1 SEM. Histogram bars with the same fill pattern are not significantly different from each other (LSD, $p<0.01$).

Discussion

In this paper we report the outcomes of experiments designed to test the eicosanoid hypothesis in the American cockroach, *P. americana*. The results of all experiments support the hypothesis. First, treating experimental cockroaches with dexamethasone prior to infecting them with bacteria significantly reduced nodulation at all points in the time course experiments. Second, the influence of two eicosanoid biosynthesis inhibitors, phenidone and esculetin, on nodulation was expressed in a dose-dependent manner. Third, seven different eicosanoid biosynthesis inhibitors significantly reduced nodulation when compared to control treatments. Finally, the influence of dexamethasone on nodulation was reversed by treating infected cockroaches with arachidonic acid, an eicosanoid precursor polyunsaturated fatty acid. Taken together, these four separate lines of evidence strongly support the overall hypothesis.

The results of the time course experiment indicate that cockroaches treated with dexamethasone produced significantly fewer nodules than the control cockroaches at all time points in the experiment. We infer from this finding that inhibition of eicosanoid biosynthesis influences the cellular events involved in nodulation early in the infection process, and continues to exert a negative influence for many hours PI.

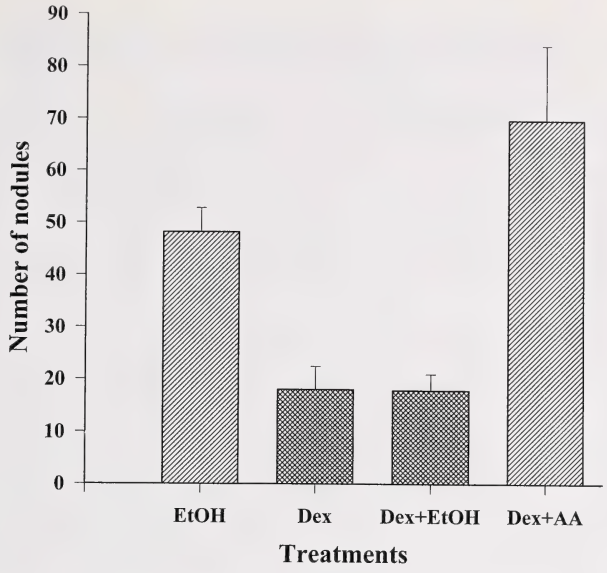

FIGURE 5. Eicosanoid-precursor fatty acids reverse the effect of dexamethasone on nodulation in adults of *Periplaneta americana*. Cockroaches were treated with ethanol (EtOH) or dexamethasone (Dex) and then intrahemocoelically infected with approximately 5 x 10^5 cells of the bacterium, *Serratia marcescens*. Immediately after infection, test insects were treated with 50 µg of arachidonic acid (Dex+AA). Control insects were treated with dexamethasone and ethanol (Dex+EtOH). The height of histogram bars represents the mean number of nodules found in each insect (n=6 individuals) and the error bars represent 1 SEM. Histogram bars with the same fill pattern are not significantly different from each other (LSD, $p<0.01$).

The time course experiment also indicates the upper limits of nodulation reactions to bacterial infections in cockroaches. The experimental cockroaches produced a maximum of approximately 40-63 nodules/individual by approximately 10 hours PI. This value is in line with the outcomes of similar experiments with other insect species. Larvae of the tenebrionid beetle, *Z. atratus* produced approximately 50 nodules/individual by 6 hours after infections with the same number of bacterial cells (Miller et al. 1996). The larvae of several Lepidoptera produced more nodules in response to similar challenges. Tobacco hornworms, *M. sexta* yielded approximately 120 nodules/individual (Miller et al. 1994), and silkworms, *B. mori*, formed approximately 80 nodules/individual (Stanley-Samuelson et al. 1997). In our work with another hemimetabolous species, Miller et al. (1999) recorded approximately 45 nodules in identical experiments with adult crickets, *G. assimilis*.

Howard et al. (1998) suggested that differences in nodulation intensity might be due to differences in circulating hemocyte populations. In work with tobacco hornworms and larvae of *Z. atratus*, Howard et al. (1998) recorded numbers of nodules formed in reaction to similar bacterial challenges as a function of insect size, weight and age. These experiments showed that nodulation was not influenced by these three parameters. Noting that insects tend to maintain fairly similar concentrations of circulating hemocytes (approximately 4 to 6 x 10^6 cell/ml hemolymph), those insect species with copious amounts of hemolymph, such as tobacco hornworms, would have far larger absolute numbers of circulating hemocytes. The authors speculated that if circulating hemocyte

population sizes account for differences in nodulation capacity, then it should not be surprising to record considerable differences among insect species in nodulation responses to similar infection challenges.

We conducted two independent dose-response studies for the influence of eicosanoid biosynthesis inhibitors on nodulation in response to similar bacterial challenges. Dose-response relationships are basic to physiological research, and the approximately linear negative relationships we obtained for phenidone and esculetin strongly support the idea that eicosanoids mediate nodulation reactions to bacterial infections in the American cockroach.

Due to their importance in human medicine, many different inhibitors of eicosanoid biosynthesis are available. Some, such as aspirin and ibuprofen, are available as analgesic drugs for relief of minor pains, while many others are not yet approved for use in humans. These compounds, which we refer to with the general term "eicosanoid biosynthesis inhibitors", exert different actions in cellular eicosanoid biosynthesis. For example, dexamethasone inhibits PLA_2. Dexamethasone exerts other actions, as well, including influence on gene expression. Several compounds specifically inhibit cyclooxygenase, the first step in prostaglandin biosynthesis (Fig. 1), while esculetin is a specific inhibitor of 5- and 12-lipoxygenases. Our experiments with different inhibitors showed that all seven of the compounds we tested resulted in similar reductions in nodulation. The observation that separate experiments with inhibitors of cyclooxygenase and lipoxygenase pathways similarly retarded nodulation in adult cockroaches indicate that cyclooxygenase and lipoxygenase products act in nodule formation. We interpret this finding in terms of the nodulation process. Nodulation results from complex cellular physiology which involves many separate cellular actions. Inhibiting one or more of the eicosanoid-mediated steps would be registered as reductions in the overall nodulation process. It follows that eicosanoids mediate more than one cellular step in nodulation.

The results with seven different inhibitors are subject to a slightly more subtle interpretation. Indomethacin, ibuprofen, naproxen and piroxicam are all cyclooxygenase inhibitors; however, they inhibit mammalian cyclooxygenases in slightly different ways. Moreover, phenidone is a dual lipoxygenase/ cyclooxygenase inhibitor. Again, this compound acts in a slightly different way from the other cyclooxygenase inhibitors. Hence, the observation that all of these compounds yielded similar results indicates that their actions are exerted through a common mechanism, specifically, inhibition of cyclooxygenase.

The results of the rescue experiments strongly support our hypothesis that eicosanoids mediate nodulation in American cockroaches. Dexamethasone is thought to act by inhibiting PLA_2, the enzyme responsible for releasing arachidonic acid from cellular phospholipids. This is the first and rate-limiting step in eicosanoid biosynthesis. Dexamethasone inhibits eicosanoid biosynthesis by inhibiting release of substrate from cellular phospholipids, which in effect withholds substrate from cyclooxygenase and other eicosanoid biosynthesizing enzymes. If this is so, then providing arachidonic acid to the immunity-conferring cells within the cockroaches would be expected to reverse the influence of dexamethasone on nodulation. Indeed, the arachidonic acid treatments restored the cockroaches' ability to produce nodules in response to bacterial infections.

Stanley-Samuelson (1994a) indicated that experiments with eicosanoid biosynthesis inhibitors were based, in part, on the assumption that the experimental insects were competent to biosynthesize eicosanoids. The presence of eicosanoid precursor polyunsaturated fatty acids and the enzymes responsible for eicosanoid biosynthesis have been documented in American cockroaches. Stanley-Samuelson and Pipa (1984) determined the presence of three eicosanoid precursor polyunsaturated fatty acids in several specific tissues from adult American cockroaches. Also, Jurenka et al. (1986) documented the presence of eicosanoid biosynthesizing enzymes in fat body of adult cockroaches. Hence, a basic assumption of this line of experimentation has been met.

While the data reported here represents males and females, we considered the possibility that each gender may express different reactions to bacterial infections. We recorded the sex and mass of each adult in all experiments; however, statistical analysis showed no differences in the nodulation reactions to bacterial infections in American cockroaches due to gender or mass.

Our background control experiments indicate that the nodules we recorded were due to the experimental treatments, and not to adventitious infections. Cockroaches taken directly from the colony had a low background of nodulation. The inject treatments, similarly, did not influence the low background of nodulation. Hence, the experimental protocols allow a physiological interpretation of the data: inhibition of eicosanoid biosynthesis impairs cockroach immunity.

Finally, the hypothesis that eicosanoids mediate cellular immunity in cockroaches takes on broader significance in mechanisms of signal transduction in invertebrate immunology. While eicosanoids were the first biochemical signal moieties discovered in insect cellular immune reactions (Stanley-Samuelson et al. 1991; Stanley 1999), they are not the sole mediators of cellular immune reactions in insects, nor other invertebrates. Downer and his colleagues have shown that biogenic amines are involved in hemocytic reactions, including phagocytosis, nodulation, and cellular movements (Baines et al. 1992; Baines and Downer 1994; Diehl-Jones et al. 1996). These works suggest that eicosanoids and amines are essential in overall cellular defense processes. Certainly, other, still unknown, biochemicals will be found to exert important actions in invertebrate cell defense reactions.

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FIRST CANADIAN RECORD OF THREE PARASITOID SPECIES (HYMENOPTERA: BRACONIDAE: EUPHORINAE) OF THE TARNISHED PLANT BUG, *LYGUS LINEOLARIS* (HEMIPTERA: MIRIDAE)

A.B. BROADBENT[1], H. GOULET[2], J.W. WHISTLECRAFT[1], S. LACHANCE[3] and P.G. MASON[2]

The tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) is a major pest of many vegetable and tender fruit crops and an occasional pest of forage and greenhouse crops in Canada. Three species of braconid endoparasitoids are known to attack *Lygus* nymphs in eastern Canada: *Peristenus pallipes* (Curtis), *P. pseudopallipes* (Loan), and *Leiophron lygivorus* (Loan) (Loan 1980). However, releases of the European parasitoids, *Peristenus digoneutis* Loan (Day et al. 1990; Day 1996) and *P. conradi* Marsh (Day et al. 1998) into the northeastern US and their subsequent establishment in 1984 and 1988, respectively, created the potential for these species to eventually enter Canada as additional biological control agents of *Lygus* spp.

As part of a Canadian project to investigate the potential introduction of European parasitoids to control *Lygus*, field collections of *Lygus* nymphs made in southern Ontario and southern Quebec during the summers of 1998 and 1999 were brought to the Southern Crop Protection and Food Research Centre (SCPFRC) in London to assess percent parasitism (based on 10–20 dissected nymphs) and to rear parasitoids to the adult stage for species identification. In addition to collections of the native parasitoids, *P. pallipes, P. pseudopallipes*, and *L. lygivorus* from *Lygus* hosts, the following three species were collected for the first time in Canada in 1998: *P. digoneutis, P. conradi* and *Leiophron uniformis* Gahan (voucher specimens of each species were deposited in the Canadian National Insect Collection, AAFC, ECORC, Ottawa after identification by H. Goulet). Table I lists the collection data: location, geographic coordinates, crop, dates collected, dates of parasitoid emergence and number of specimens emerged. In 1998 the one specimen of *P. digoneutis* collected from *Lygus* entered diapause after exiting from the host and emerged as an adult in June 1999, 13 days after removal from 2°C cold storage. In 1999, 6 adult *P. digoneutis* emerged 19–28 days after collection, as expected because this species is bivoltine. *Leiophron uniformis* is also multivoltine whereas *P. conradi* is univoltine.

Peristenus digoneutis and *P. conradi* were both found south of Montreal, within 50 km of the New York border in a vegetable/forage crop region of Quebec. The farm at St. Constant is approximately 30 km north of the AAFC Research Farm at Ste. Clothilde (20 km north of the US border). Day et al. (1998) had projected, based on widespread collections of *P. digoneutis* in the northeastern states and due to prevailing winds, that this species would likely disperse into Quebec in 1996. However, *P. conradi* had not been collected in as wide an area of the northeast US, and was only first recovered in the southern part of NY in 1993 (Day et al. 1998). *P. conradi* was therefore unexpected in Quebec in 1998. *Leiophron uniformis* is common and widely distributed throughout the US on all major species of *Lygus* and on *Halticus bractatus* (Say), the garden fleahopper, which is thought to be its preferred host (Day and Saunders 1990). This braconid had not been recorded in Canada until our 1998 collection.

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TABLE I. First records for three species of braconid parasitoids collected from *Lygus lineolaris* in eastern Canada in 1998 and 1999.

Species	*Leiophron uniformis*	*Peristenus digoneutis*	*Peristenus conradi*
Location	AAFC, SCPFRC farm, London, ON	AAFC farm, Ste. Clothilde, PQ	Farm, St. Constant, PQ
Geographic coordinates	43°01.77 N 81°12.33 W	45°10.05 N 73°40.53 W	Not recorded
Crop	Weedy alfalfa	Weedy alfalfa	Alfalfa
Date collected	9 June, 24 June, 2 July, 14 July 1998	i) 19 June 1998 ii) 30 June 1999	19 June 1998
Date emerged	26 June – 24 July 1998	i) 16 June 1999 ii) 19–28 July 1999	13 & 14 April 1999
No. parasitoids emerged	1, 6, 3, 3	i) 1 ii) 6	2
No. *Lygus* nymphs collected	200, 135, 141, 170	i) 400 ii) 1500	60
% Parasitism from *Lygus* nymph dissection	37.5, 8.3, 0, 0	i) 26.7 ii) 19.4	Not recorded

Future plans include tracking the distribution of *L. uniformis* and the distribution and impact of the two European species on *Lygus* populations in eastern Canada. The introduction of one or both of these parasitoids into Ontario is also planned.

Acknowledgments

We gratefully acknowledge the technical support of Lola Gualtieri and Lou Verdon (AAFC, SCPFRC, London) and Mike Sarazin (AAFC, ECORC, Ottawa).

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BOOK REVIEWS

Northeastern Tiger Beetles. A Field Guide to Tiger Beetles of New England and Eastern Canada 1999 *by* J.G. Leonard and R.T. Bell. CRC Press, Boca Raton, FL. 176pp. ISBN 0-8493-1915-3

Although the book's title would indicate that it deals only with NE Nearctic cicindelids, the book is essentially a primer on tiger beetles divided into sixteen sections.

The first three sections introduce the authors, give their backgrounds, and acknowledge those individuals and institutions that provided assistance with the project.

Following that, are sections dealing with the definition of a tiger beetle, definitions of what constitutes a species, and tiger beetle ecology. Ensuing sections deal with methods of capturing tiger beetles, curation of specimens and keys to adults and third-instar larvae. The keys are amply illustrated, especially the one dealing with larvae. Following the keys are sections dealing with the rearing of tiger beetles and their conservation in the field.

The species accounts that follow the above are broken down by the species' phenotypic expression (i.e., "GREEN SPECIES" or "DARK SPECIES WITH COMPLETE WHITE MACULATIONS", etc.) and each taxon has a brief adult and larval description, habitat preference, life cycle, geographic range and notes – where known. Each taxon also has accompanying range maps, showing its range within New England and eastern Canada. Also included within the species account sections are four pages of color plates illustrating twenty-four taxa.

The final four sections include a glossary of terms, references and suggested reading, an index and several blank pages for field notes.

My only criticisms of the book are related more to presentation than to content. An example would be Figure 6 (ventral view of *Cicindela sexguttata*), which is used to illustrate and identify ventral body segments. The figure makes no mention of epimera, mesosternum or episterna other than the proepisternum. Other examples involve the illustration of labra. The traditional method of illustrating a cicindelid labrum is to show it in dorsal aspect, with the labral dentition on the upper portion of the illustration. For some reason Leonard and Bell have chosen to display all labra in frontal aspect with the dentition on the bottom. Labral Figures 24 and 25 are credited to Willis (1968), but they are actually upside-down when compared to the way they appeared in that paper. These small glitches do little to diminish the quality of the book, but they should have been corrected during peer-review or editing.

This is an excellent source book for any novitiate with an interest in the Cicindelidae and should be on the shelf of any cicindelophile – if for no other reason than to reinforce why we study these fascinating beetles.

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Catalogue of the Tiger Beetles of Canada and the United States 1999 *by* Richard Freitag. NRC Research Press, Ottawa, ON. 195 pp. ISBN: 0-660-17640-8. Paper. $39.95 Can.

Dr. Freitag has given us a remarkably comprehensive bibliography of the North American tiger beetle fauna. He includes over 2400 references, far more than I would have thought existed. For each subspecies and for each species in which subspecies are not recognized, there are the following entries: type locality; range within North America; synonyms, each with type locality, its sex and its type depository; and the same information for the type of the valid name. The remaining references are grouped under the following headings: immature stages, taxonomy, re-description (if applicable), biology, and habitat. The category "taxonomy" is interpreted relatively broadly to include mention in regional lists, locality records, inclusion in other bibliographies, among other types of works. The number of references to some of the commoner species is staggering; those for *Cicindela sexguttata* occupy almost all of two pages.

There is also a useful treatment of Cicindelinae as a whole, including about a hundred papers of broad scope with a code indicating the categories of information in each entry. There is a similar list for each genus. The species of *Cicindela* are listed in alphabetic order within each of Rivalier's genera (ranked as subgenera by Freitag). Some will be annoyed by this, finding a complete alphabetical treatment of *Cicindela* as a whole more convenient. As I am interested in the family tree of tiger beetles, I don't mind learning Rivalier's ideas.

It is an unfortunate fact of life that all comprehensive works are already out of date when they roll off the presses. This book is no exception: the most recent references within it date from 1997, and tiger beetle research continues to blossom, as can be confirmed by a glance at any recent number of the journal Cicindela.

Freitag's catalogue is a necessity for any entomologist contemplating work on tiger beetles. It would also be valuable for researchers with a broad interest in such topics as behavior, ecology, and evolution of insects in general. I prize it as a key to the North American tiger beetle literature, and I keep it next to the Bousquet and Larochelle 1993 Catalogue of the Geadephaga. The Freitag work has a high standard of accuracy; I have been unable to locate a single typographical error (although, of course, I was unable to check every page number and date). He has found many rare and poorly known references. I recommend this catalogue enthusiastically and without reservations.

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Interrelationship Between Insects and Plants 1998 *by* Pierre Jolivet. CRC Press, Boca Raton, FL. 336 pp. ISBN 1-57444-052-7. Hard Cover. $59.95 US

This book (336 pages, hardcover) describes the variety of relationships between insects and plants. Following a general introduction (Chapter 1) outlining the various types of plant-insect interactions, the subsequent chapters move into more detail on a range of topics, which are as follows:

2. Plant-feeding insects and arthropods of the geological past
3. An early twentieth century classification of food plant selection among phytophagous insects
4. Relationships between insects and fungi

5. Physiology of food selection
6. Carnivorous and protocarnivorous plants
7. Myrmecophily and ant-plants
8. A rare plant-insect relationship: epizoic symbiosis
9. Galls and mines
10. Insect mimicry and homochromy in relation to plants
11. Natural weed control in the Holarctic region and in the tropics using phytophagous insects
12. Pollination
13. Coevolution (or not) between insects and plants
14. A general review of insect-plant relationships; some thoughts about learning; the canopy

Following these chapters is a two-page epilogue (Chapter 15), an extensive glossary (18 pages), 42 pages of references, and three indices: plant (10 pages), insect (8 pages) and general (12 pages).

The author clearly states in his Foreword that "This book is not on insect physiology but an essay about all aspects of the interactions between insects and plants. Its aim is to be different from the other texts in covering more topics." And in the Preface, "The present book contains topics related to insects and plants generally absent from ordinary books. There are plenty of books on physiology, chemistry and genetics of plant selection by insects, but none includes carnivorous or myrmecophilous plants, pollination, etc. You have to find that in specialized treatises." These two quotes provide perhaps the most insight into the scope of this book. This book does give generally useful information about specific plant-insect systems that are not as critically discussed in other texts. The information appears to be complete and up to date on the most recent research conducted in the specific areas discussed.

However, I did not find the book all that easy to read, as it tended to meander from topic to topic with no clear connecting thought between. Further, there are injections of non-insect examples that detracted from the plant-insect relationship being discussed that did not, in my opinion, add to the readers' understanding. The author's use of figures did not necessarily clarify the concepts being discussed. For example, the same figure (showing an aphid probing, penetrating and ingesting plant material with its stylets) would be referenced to describe how aphids feed and, later on, as a demonstration of how little is known about how insects with ovipositors select host tissue. Chapters 1 through 3 were the most difficult to read critically. From Chapter 4 onward, the chapters tended to be more focussed and flowed more logically from introduction to conclusion; however, there are some not so minor difficulties with the presentation that detracted from the main thesis.

I found several instances of spelling errors, confused tenses within sentences and in general poor sentence structure. The text fluctuates from a scientific exposition on plant-insect interactions to a loosely structured free-flowing dialogue, analogous to that of a brainstorming session. Less than half the chapters are concisely put together, well written and clear; the rest are heavily interspersed with unrelated rambling tangents. On the whole it is a text which will provide many helpful directions for those in the plant-insect interactions field but cannot be taken as the sole authority on any given interaction or as a stand-alone book, as the author himself so clearly pointed out.

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Agricultural Chemicals Book I – Insecticides, Acaricides and Ovicides 1998 *by* W.T. Thomson (14th Revision). Thomson Publications, Fresno, CA, USA. xxiv + 270 pp. ISBN: 0-913702-33-1. Paper. $24.95 US

This volume will prove a useful reference for pest managers seeking preliminary information about possible control agents for insect and mite pests. The book begins with brief instructions on how to use the manual. A comprehensive index follows and contains nearly 2,000 entries. The major portion of the manual briefly describes insecticides, acaricides and ovicides either available or under development around the world. This portion of the text comprises seven sections: cyclo compounds and organic metal compounds; carbamates; animal plant derivatives, synthetic pyrethroids, and inorganic compounds; diphenyl compounds and other non-phosphate insecticides; and, three groupings of organic phosphates. The Glossary that follows contains pointers on sprayer calibration and a number of useful conversion tables and formulae. Also included in the Glossary are tables of standard weights and metric equivalents. If one wanted to learn the number of "grains" in a "scruple" and the number of "scruples" in a "dram", one would turn to the Glossary. A comprehensive list of addresses of the basic manufacturers of compounds listed in the manual forms the final chapter.

The agrochemical industry is continually evolving as pesticide registrations are expanded, experimental materials are registered and new compounds are synthesized or discovered and enter the development process. W.T. Thomson has attempted to keep his publications as up to date as possible; the current release is the 14th revision of the manual. Since the volume attempts to list all control agents for insects and mites in use or in development around the world, reference to each must be cursory at best. Nonetheless, for each listing, the reader will find: the common name; known trade names; the structural formula; origin and brief information on toxicity; formulations available; known phytotoxicity; uses; rate range; and, limitations and precautions. This manual is only intended to be a starting point in a search for information for a particular control agent. In every case, the label is the only definitive source of information and must be carefully consulted before recommendations can be made.

Anyone who has learned only the name of a particular control agent and desires a bit more information will find this volume particularly useful. If either a common name or a trade name is known, a quick scan of the index should lead to that information. Indeed, the index will be the most frequently consulted portion of the book as materials within each section are not listed alphabetically. This book is not designed for anyone seeking information about control of a specific pest on a specific crop; indexes of pests and crops have not been prepared.

Organization of the book is its greatest limitation. Compounds can be readily located only by consulting the index. There is no apparent order of listings within sections. Also, while most application rates are specified in metric units, rates for many of the older materials are listed in units of the U.S. Customary system. Consistency would reduce the potential for error. Finally there are a number of minor typographical errors throughout the text. Nonetheless, Agricultural Chemicals – Book I is a reasonably priced, relatively complete and concise source of information for insecticides, acaricides and ovicides. On the pest manager's shelf, the volume will prove a useful place to start a search for information about an unfamiliar pest control agent. The manual provides sufficient information to allow a searcher to locate and request a product label – the definitive source of product information.

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***Geologische und biologische Entomoökologie der rezenten Seidenbiene* Colletes. (tr. Geological and biological ecology of the extant silk bees [genus *Colletes*])** 1997 *by* D. Mader. Logabook, Cologne. 807 pp. ISBN 3-87361-263-1. Hardcover. $50.00 Euro

The following is not intended to be a review, rather it is a synopsis of the contents of Dr. Mader's book. This large volume (807 pages, A7 format, hardcover), written entirely in German, is the first of two volumes detailing the nesting and foraging ecology of primarily *Colletes daviesanus*, with other examples from the family Colletidae and other solitary members of the order Hymenoptera.

After a short introduction outlining the morphology and various types of nest structures made by *C. daviesanus* and a small selection of solitary bees and wasps comes section two, the meat of the book. It is divided into several subsections as follows (notes in parentheses are not in the German text, and are given here for descriptive purposes):

2.1 Substrate preparation and nest construction.
2.2 Substrate types (rock species and formations) and nest site environment (divided into palaearctic, nearctic and neotropical species).
2.3 Nest site choice in reference to substrate characteristics (drainage, sun exposure, etc.).
2.4 Colonial and solitary nesting.
2.5 Geology of nest substrates (sedimentology and palaeogeography, etc. with emphasis on Germany and Europe including western Russia and the Baltic states). Included in this section are descriptions of anthropogenic substrates.
2.6 Construction of the silk nest linings.
2.7 Botanical environment and flower visiting ecology (divided into palaearctic, nearctic and neotropical species of *Colletes*).
2.8 Kleptoparasites and predators.
2.9 Use of *C. daviesanus* nests by *Osmia adunca* and other *Osmia* species.
2.10 Long-term population dynamics of nesting sites (mostly within Germany).
2.11 Selected bibliography of nest construction and/or nest substrates.

The last parts of the book are 64 pages of references and a 132-page index.

The book is profusely illustrated (over 450 illustrations in black-and-white, colour, line drawings, and charts) but even to someone fluent in German, the length of the text may seem daunting. Non-fluent readers of German should expect difficulties with the text; it is full of classic German extended sentence constructions. As a reference work on its topic it is superlative, and it presents a complete (especially when the second volume due in the year 2000 is included) description of the natural history and nesting ecology of *Colletes*. Even if the emphasis is at times centred on Europe or Germany, the book includes enough mention of species found in other geographical areas to be of interest to workers outside Europe.

MARTIN DAMUS

1999 ANNUAL MEETING

The **Entomological Society of Ontario** is grateful for the support received for the **Annual General Meeting** held in Toronto on 15-17 October 1999 from: Agrevo, Cyanamid Crop Protection, Dow Agro-Sciences Canada Inc., DuPont Canada Inc., McDonald's Restaurants, Metro Toronto Zoo, Novartis Crop Protection Canada, Pizza Pizza, Rhone Poulenc and United Agri Products.

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